

Natural variation in coral reef trophic structure across environmental gradients

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Frontiers in Ecology and the Environment

DOI:
[10.1002/fee.2144](https://doi.org/10.1002/fee.2144)

Published: 01/03/2020

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Heenan, A., Williams, G., & Williams, I. (2020). Natural variation in coral reef trophic structure across environmental gradients. *Frontiers in Ecology and the Environment*, 18(2), 69-75.
<https://doi.org/10.1002/fee.2144>

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Title: Coral reef trophic structure naturally occupies the middle ground

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Abstract

Policies to tackle today's fisheries sustainability challenges generally utilize an ecosystem approach, one that incorporates interactions between fishes, fishers and the environment. Fishing alters coral reef fish trophic structure, but properly assessing those impacts requires an understanding of how and why that structure varies naturally across scales. Using a combination of small-scale and large-scale surveys we generate biomass pyramids for 21 uninhabited Pacific islands, concluding: (1) the distribution of reef fish biomass across trophic levels is highly scale dependent; trophic structures that appear top-heavy at small scales can take a variety of different states when data are integrated across the broader seascape; (2) reefs can be 'middle-driven', forming 'convex' systems with greatest biomass at intermediate consumer levels and; (3) in unfished coral reef systems, trophic structure is strongly predicted by energy into the base and middle of the food web, as well as the interacting effect of temperature.

Introduction

With approximately 20% of the world's 7 billion people living in the coastal tropics, the dependence upon and vulnerability of small-scale fisheries is high (Bell *et al.* 2009; Sale *et al.* 2014; Golden *et al.* 2016). Coral reef ecosystems and their associated fisheries are impacted by climate-change, habitat degradation and fishing (Mora *et al.* 2011; Bell *et al.* 2013; Hughes *et al.* 2017; Cinner *et al.* 2018), stressors that are predicted to intensify (Cheung *et al.* 2010). Adaptations to maintain the food security of coastal communities might include the transfer of fishing effort over to more productive species (Robinson *et al.* 2019), while limiting the harvest of species that perform critical ecosystem functions, like herbivory (Bell *et al.* 2013; Chung *et al.* 2019). However, environmental gradients also drive substantial variation in reef ecosystem configurations (Williams *et al.* 2015, Heenan *et al.* 2016). Management, such as catch limits, or fisheries baselines, must therefore account for these natural bounds set by reefs' environmental contexts.

Although few marine ecosystems are completely unaffected by humans (Halpern *et al.* 2008), minimally impacted ecosystems offer insight into natural ecological limits. Among those are remote Indo-Pacific coral reefs located several hundreds of kilometres from the nearest human population centres. Studies from these near-pristine ecosystems can inform benchmarks of ecosystem status suitable for fisheries management (Holt and Irvine 2013). For example, that the fisheries potential of

subtropical reefs is lower than tropical ones (McClanahan *et al.* 2019). From microbes through to top predators, natural gradients in wave energy, temperature and primary production are key determinants of coral structure and function (Williams *et al.* 2019).

The standing biomass of reef fishes can double along gradients of increasing oceanic productivity, and accounting for this is key to quantifying fishery depletion (Williams *et al.* 2015). Similarly, differences in temperature along a subtropical to tropical gradient have substantial effects on the functional composition of herbivorous fish assemblages (Heenan *et al.* 2016). Collectively, incorporating environmental and habitat drivers, such as those along with coral cover and wave exposure, greatly improves our ability to estimate local carrying capacity and thus scope for recovery (Goropse *et al.* 2018, Harborne *et al.* 2018). More generally, studies of remote reefs have reported highly variable trophic structure. Those include bottom-heavy systems in the Indian Ocean (Graham *et al.* 2017b), as well as extremely upper-trophic level dominated 'inverted pyramids' on some Pacific reefs (Friedlander and DeMartini 2002; Sandin *et al.* 2008; DeMartini *et al.* 2008). However, it is not clear how much and in what ways variability in coral reef fish assemblage trophic structure is driven by environmental factors. This warrants attention as the basis for robust small-scale fisheries management accounting for environmental context.

We tested whether the trophic structure of coral reef fish assemblages is related to temperature, as has been shown for temperate marine systems (Frank *et al.* 2007), and energetic setting (i.e. oceanic production and irradiance). Primary production in the coastal ocean is limited by sunlight, which decreases with depth and latitude (Campbell and Aarup 1989). Light influences benthic primary producers on coral reefs (Gattuso *et al.* 2006) and high irradiance is linked to increased fish biomass (McClanahan *et al.* 2019). How this affects consumers and, ultimately, trophic structure remains unknown. Energetic subsidies from outside the defined ecosystem appear to facilitate increased biomass in upper trophic levels (McCauley *et al.* 2018), as coral reef planktivore and piscivore biomass is positively related to nearshore oceanic production (Williams *et al.* 2015). A recent multi-method study emphasized the importance of both pelagic and cryptobenthic energy pathways in supporting coral reef fish assemblage productivity (Morais and Bellwood 2019). It has also become clear that small-bodied cryptic fishes such as blennies and gobies are a key energetic resource sustaining overall reef fish production (Brandl *et al.* 2019). Because of their low detectability in visual surveys (Kulbicki *et al.* 2010), these small fishes tend to be grossly underestimated by survey programs. Thus, there is not only high natural variability in reef fish trophic structure, but also potential for method choice to impact conclusions about the status and role of different ecosystem components in driving overall production.

Here we integrated data from two co-located methods, a conventional survey method for which divers record all fishes within small areas, with a broader-scale survey that targets larger-bodied, roving, and generally rare or patchily distributed species not well sampled by smaller-scale methods (Richards *et al.* 2011). We did this at 21 remote islands and atolls (hereafter 'islands') that are largely isolated from direct human impacts to i) document the degree of variation in trophic structure among different reef ecosystems, and; ii) quantify the environmental drivers of this variation. Understanding the sources of uncertainty introduced by method choice, alongside the natural constraints set by coral reefs' energetic settings, will improve scope to identify sustainable levels of fisheries exploitation and recovery potential.

Panel 1. The artefacts of measurement scale in community assessments

It has long been recognised that scale determines the range of ecological patterns and processes described by a study (Wiens 1989). Yet, few investigations provide biological justification for the scale

at which measurements are taken (Jackson and Fahrig 2015). Indeed ecologists frequently generalize their findings beyond the scale of observations, as part of a wider tendency to underappreciate scale-related ecological issues (Estes *et al.* 2018). When studying a single species, the extent and grain size (size of individual units of observation units - i.e., quadrat or transect) can be matched to the scale at which inferences are made (Wiens 1989). However, that is not feasible when conducting ecosystem-wide assessments involving multiple species. From blennies to barracuda, the resource patch size of the multitude of species within an ecosystem varies considerably. Also, traits, such as home range, school size, swimming speed, mobility, curiosity, coloration, patterning, and whether species are cryptic or not, impact detectability and introduce sampling bias (Kulbicki *et al.* 2010). When observations are collected at a scale that doesn't align with the variety of species within an ecosystem, results can be confounded by artefacts of measurement scale, undermining ability to identify real patterns and processes. As such, there is no single 'best' scale or method for ecosystem-wide surveys.

One potential approach is to use multiple survey methods differing in scale. Here, we surveyed fish communities using two *in situ* methods of contrasting grain size (WebPanel 1). The stationary point count (SPC) surveys all species observed within paired 15 m diameter cylinders (total area 352 m² per survey). The second method, the towed-diver survey, targets large-bodied (> 50 cm TL) and roving species within a bigger survey area (averaging ~2.2 km long * 10 m-wide).

Of the ~600 taxa recorded, 66 were recorded on both method (WebTable 1). These species included large-bodied low trophic level species (parrotfish and surgeonfish), massive mid-trophic planktivorous species (Manta rays), and predators (barracuda, groupers, jacks and sharks). Some fishes, such as the semi-cryptic sabre soldierfish (*Sargocentron spiniferium*) were rarely recorded by either method, and possibly neither methods censuses them well. For most of those species, encounter rates were lower but densities higher on SPC compared to tow surveys (WebTable 1). The lower encounter rates, particularly of rare species, reflect differences in the total area covered per method (total area surveyed on SPC ~ 37 hectares and tow ~2130 hectares) and introduces high uncertainty in their density estimates (Jennings and Polunin 1995). For example, 120 manta ray (*Mobula spp.*) were observed on tow, compared to 25 on a similar number of SPC surveys. The tow estimate of biomass for this species at Baker island of 20.9 +/- 9.8 g m⁻², is less than half the estimates from SPC (45.9 +/- 39.2 g m⁻²) as well as being much less variable. Conversely, for a few species, such as the camouflage grouper (*Epinephelus polyphekadion*) and longface emperor (*Lethrinus xanthurus*), encounter rates were 7-70 times higher on the SPC, and density estimates 75-120 times higher (WebTable 1). This is likely due to those species being much easier to detect by SPC divers, carefully searching small areas, than by constantly moving tow-divers travelling approximately 1 m above the bottom.

For some fishes, like the Giant trevally (*Caranx ignobilis*) and Great barracuda (*Sphyraena barracuda*), the SPC encounter rate was similar to that of the tow (0.76-0.88), but density estimates were ~ fifty times higher (i.e. similar numbers seen in much smaller areas). Other species that were ~ half or less frequently encountered on SPC, including the Galapagos shark (*Carcharhinus galapagensis*), bluefin trevally (*Caranx melampygus*) and green jobfish (*Aprion virescens*) had SPC biomass estimates ~25-60 times tow estimates (WebTable 1). High estimates on SPC are likely driven by attraction of some species to divers (Parrish and Boland 2004), which can lead to systematic overestimates in density, particularly for small-areas surveys involving stationary divers (Colvocoresses and Acosta 2007). Notably, the initial 5 min species listing period of the SPC provides an opportunity for roving predatory fishes to aggregate around divers, as observed at some remote locations (Parrish and Boland 2004). Generally, towed diver surveys generate much lower estimates

of shark and jack density than smaller-scale belt transects (Richards *et al.* 2011). Rather than ignoring, or simply removing species that are poorly estimated by SPC, which is the typical approach to these artefacts of scale and method bias (MacNeil *et al.* 2015; Williams *et al.* 2015), here we merge the SPC and tow survey data. By doing so, we selectively use both datasets to address known biases of the methods. A key benefit of this approach is that it allows us to include all observed coral reef fish species in our analyses.

Methods

Reef fish community surveys – integrating multi-scaled data for a community perspective

We used fish survey data collected using two methods at 21 uninhabited islands in the western central Pacific; the stationary point count (SPC) and the towed diver technique (Panel 1, WebPanel 1, Figure 1A). From 1034 SPC surveys and 985 towed transects, we calculated individual species biomass using their observed size, abundance and published length-weight relationships (Kulbicki *et al.* 2005). Trophic levels were then assigned from FishBase (Froese and Pauly 2016).

The process to integrate the survey data was based on several assumptions; i) learned diver avoidance behaviour was minimal, as these were extremely remote systems, where fishes had few previous interactions with people (Januchowski-Hartley *et al.* 2011); ii) attraction to divers was least for the tow method, as towed-divers constantly move at $\sim 3 \text{ km hr}^{-1}$, surveying ahead of them; iii) species that were rarely encountered on the SPC are generally poorly estimated by that method. Broadly, we largely assume that small-scale SPC density estimates are most accurate for small and common fishes, but tow is generally more suitable for large-bodied and rare fishes.

Given these assumptions, and following a sensitivity analysis on a range of encounter and density ratios (WebPanel 1, WebTable 2), the criteria for integrating species observations from those methods were: 1) for all observations of species observed on both tow and SPC, we used SPC data for fishes smaller than 50 cm; 2) for fishes $> 50 \text{ cm TL}$ we used; a) the tow dataset when confident we overcount a species with SPC (> 5 density of tow); b) the tow dataset for species that are very rarely encountered by SPC (SPC encounter rate is $< 1/5^{\text{th}}$ of the tow rate); c) the SPC dataset when we are confident tow undercounts (SPC density is $< 1/5^{\text{th}}$ of the tow density). To assess the difference between the biomass estimates per trophic level from just SPC, compared to the integrated data based on the merging criteria, we visually inspected island-level plots of proportional and absolute biomass per trophic level.

Variation in trophic structure

To understand how the amount of biomass in each trophic level bin varied with absolute total fish biomass, we fitted generalized linear mixed effects models of proportional biomass per trophic level as a function of total fish biomass (g m^{-2}). The random effect was marine province (Hawaii, Central Polynesia, Tropical Northwest Pacific (Spalding *et al.* 2007)

Many islands lacked species in the 2.5-3, and 3.5-4 trophic bin, so we grouped trophic levels, 2-2.99 (referred to as 2), 3-3.99 (3) and > 4 (4). There was a clear increase in absolute biomass of planktivorous species (trophic level 3) at islands with high total fish biomass (Figure 2, WebPanel 2). A metric multi-dimensional scaling (MDS) of the proportional contribution of individual species to

trophic level 3 biomass per island was used to identify key species in that trophic level. The MDS was based on a Euclidean distance matrix, and overlaid vectors represent Pearson's correlations (threshold ≤ 0.7) of the original species variables with the ordination axes, with vector length proportional to correlation strength.

Biophysical drivers of coral reef fish trophic structure

We fitted generalized linear models to investigate the influence that external energy inputs (sunlight and oceanic productivity) and temperature had on biomass in each trophic level. Specifically, we modelled biomass as a function of irradiance (Einsteins $\text{m}^{-2} \text{d}^{-1}$), sea-surface temperature ($^{\circ}$ Celsius) and chlorophyll-a (mg m^{-3}) - a proxy for phytoplankton biomass and thus oceanic primary production. These biophysical drivers were island level satellite-derived climatologies (long-term means) (Gove *et al.* 2013). All models were fitted in R (www.r-project.org). Model fitting, selection and assessment of model performance process are detailed in WebPanel 3.

Results

The influence of reef fish survey sampling scale on trophic biomass estimates

The tendency for the SPC data to overestimate higher trophic level piscivores was evident when biomass pyramids generated from the SPC data were compared against the integrated SPC and tow data (summarized Figure 1; all islands in WebFigure 1). Top-heavy fish communities (more biomass at trophic level 4 and above than below) were evident at 11 islands for SPC data alone (WebFigure 2). When the data were integrated, only one island, Swains, exhibited trophic inversion (Figure 1). This result was robust to a wide range of decision criteria used to merge the two datasets (WebTable 2); the pooled dataset was therefore used for all subsequent analyses.

Variation in trophic structure

Considerable natural variation exists in fish assemblage trophic structure on coral reefs (Figure 2). The mean proportion of biomass in trophic levels 2-3 was 0.39, ranging from ~ 0.20 (at Howland, Baker, Jarvis and Kingman in Central Polynesia), to 0.6 at Kure Atoll in the Northwestern Hawaiian Islands, the most northerly location surveyed (Figure 2). Swains Island had the lowest proportion of biomass in the mid-trophic levels (0.32), relative to the all island mean (0.38), while Baker Island had over half of the total biomass in the mid trophic levels. Across all islands, the mean proportion of biomass in trophic level 4 and above was 0.22 (range: 0.06 at Kure to 0.43 at Swains). Total fish biomass varied greatly among islands, from 31 g m^{-2} ($\pm 6 \text{ SE}$) (Lisianski) to 140 g m^{-2} (± 36) (Jarvis) (Figure 2). The proportion of biomass in low trophic levels (2-3) decreased with total fish biomass (WebPanel 2, T-value = -2.39, p-value = 0.03), while the proportion of mid-trophic level biomass (3-4) increased (T-value = 2.11, p-value = 0.05) (Figure 2). Locations with highest total biomass (Kingman, Jarvis, Baker, Howland and FDP), had high biomass of trophic level 3 species. This included the planktivorous rays *Manta* spp. and anthias (*Luzonichthys whitleyi* and *Pseudanthias olivaceus*), small wrasses *Anampses meleagrides* and *Labroides didimatus*, sweepers *Pempheris oualensis* and fusilier *Caesio teres* (WebPanel 2). The proportion of biomass in trophic level 4 and above did not vary predictably with total fish biomass (T-value = 0.37, p-value = 0.71).

Biophysical drivers of coral reef fish trophic structure

The biophysical parameters of a reef - temperature, irradiance and oceanic primary productivity – were important predictors of fish assemblage trophic structure (WebPanel 4). However, the direction

of their effect differed among trophic levels, and in some cases was dependent on one and other. With the exception of trophic level 2 biomass, there were clear best performing models in the model sets (WebPanel 4). The explanatory power of the models of the trophic level 2 biomass was relatively poor (adjusted R-squared: 0.23), suggesting the importance of drivers not considered in this analysis (WebPanel 4). Overall, a substantial amount of variation in lower and upper trophic level biomass was associated with these three terms (proportional models adjusted R-squares > 0.70). The proportion of biomass in trophic level 2 increased with irradiance and decreased with temperature, with an interacting effect between irradiance and oceanic primary production (adjusted R-squared: 0.76, WebPanel 4, Figure 3). In contrast, the degree to which reefs were top-heavy (more biomass in trophic levels 4 and above) increased with temperature. This was true in absolute and proportional terms for trophic level 4 (WebPanel 4, Figure 3). Fish communities were more top heavy on coral reefs with warmer water and higher oceanic primary production, but this effect of temperature was diminished in the most productive locations (WebPanel 4). Absolute mid-trophic level biomass was closely positively associated with oceanic primary production (Akaike weight 0.6, marginal R-squared: 0.84) (WebPanel 4). Similar to trophic level 4, the proportion of biomass in mid trophic levels increased with temperature, and decreased with irradiance, but again this was conditional on oceanic primary production; the effect of irradiance was lower in more productive locations.

Discussion

Using a multi-method approach to synthesize data from 21 remote Pacific islands, we show considerable variation in reef fish trophic structure and carrying capacity varying in relation to oceanic context. Thus, trophic structure of fish assemblages on remote coral reefs can take a variety of forms. These include recently described 'concave' shapes indicative of bottom-driven systems (Graham *et al.* 2017), as well as, 'convex' systems with greatest biomass at intermediate consumer levels. We present the first evidence of such 'middle-driven' systems for coral reefs.

Like all complex multi-dimensional structures, inferences on the ecosystem properties of coral reefs are sensitive to the choices made about the scale of observation. This is because individual species interact with their environment in ways that vary in space and time, meaning there is no single correct scale to observe and describe an ecosystem (Levin 1992). For example, spawning aggregations that attract and concentrate predators can lead to temporarily inverted trophic pyramids that would not exist outside of this specific temporal period (Mourier *et al.* 2016). Such inverted pyramids have been reported from small-scale surveys on remote coral reefs (Friedlander and DeMartini 2002; Sandin *et al.* 2008; DeMartini *et al.* 2008), prompting debate on their theoretical feasibility (Trebilco *et al.* 2016; Woodson *et al.* 2018), and criticism that they arise as an artefact of sampling bias (Bradley *et al.* 2017; McCauley *et al.* 2018). However, few have considered the explicit role of sampling scale in how we understand what is natural, or how such patterns change across the broader seascape.

Given the variety of reef fish life histories and how that impacts their detectability (Kulbicki *et al.* 2010, Ruppert *et al.* 2018), it seems unrealistic to quantify the trophic structure of reef fishes at a single scale. We therefore integrated data at two scales (approximately meters and kms) to show that estimated reef fish trophic distributions were highly scale dependent, and also that trophic structure varies widely among locations due to differences in environmental drivers. Our results highlight the need to consider scale when making community-wide inference. Integrative multi-scale approaches are especially important to provide a full ecosystem perspective for fisheries management.

Recent studies have demonstrated how substantially humans can alter the trophic organization of coral reef fish assemblages (Sandin *et al.* 2008; DeMartini *et al.* 2008; Graham *et al.* 2017a; Ruppert

et al. 2018; McCauley *et al.* 2018). What has been lacking is an understanding of how gradients in natural environmental drivers simultaneously or independently impact spatial variation in reef fish assemblage structure. One finding of our study is that bottom-heavy pyramids were associated with higher light availability. Similar to other benthic primary producers whose distributions are limited by light intensity (Gattuso *et al.* 2006; Muir *et al.* 2015), coral reefs have a greater proportion of the reef fish biomass in low trophic levels at areas with high irradiance. Presumably, primary consumers benefit from the higher rates of benthic primary production as increased irradiance bolsters the base of the food web. Higher fisheries production in tropical coral reefs than in the subtropics is in part due to higher solar radiation (McClanahan *et al.* 2019). Thus, coral reef fisheries that target lower trophic levels may be more viable where energy into the base of the food web is higher and therefore where fish assemblages are more naturally bottom-heavy.

Our results show that the proportion of biomass in higher trophic levels is higher in warmer waters and in areas of higher oceanic primary production. Middle-driven systems - with greatest biomass at intermediate consumer levels, like those with high biomass of planktivorous species (WebPanel 2), - had greatest total reef fish biomass and capacity to sustain higher trophic levels. Coral reef predators, total fish productivity, and therefore associated fisheries, are largely sustained by pelagic and cryptobenthic energetic pathways (McCauley *et al.* 2012; Frisch *et al.* 2014; Morais and Bellwood 2019; Brandl *et al.* 2019). Together, we demonstrate that reef systems can be bottom-heavy in areas of high irradiance, and middle-driven when external energetic subsidies, delivered by a panoply of biophysical processes, are maximized. Middle-driven systems have the greatest capacity for total reef fish community biomass, and in turn greater fisheries productivity. Ecosystem-approaches to management would benefit from recognizing that coral reef trophic structures are naturally constrained to be top or bottom heavy or indeed middle-driven, and that where any one reef lies on this spectrum is influenced by the surrounding energetic environment. When setting management targets and adaptation strategies, it is vital to recognize human impacts are superimposed over natural constraints on local fisheries carrying capacity and recovery potential.

Acknowledgements

We thank Rusty Brainard for leading the NOAA Pacific Reef Assessment and Monitoring Program (RAMP) and PIFSC staff for their extraordinary efforts implementing the monitoring program. Pacific RAMP is funded by the NOAA Coral Reef Conservation Program and the Pacific Islands Fisheries Science Centre. We also thank Amanda Dillon for producing the graphic in Figure 3. This project received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 663830. GJW acknowledges internal funding from Bangor University that contributed to AH's fellowship. The contents in this manuscript are solely the opinions of the authors and do not constitute a statement of policy, decision, or position on behalf of NOAA or the U.S. Government.

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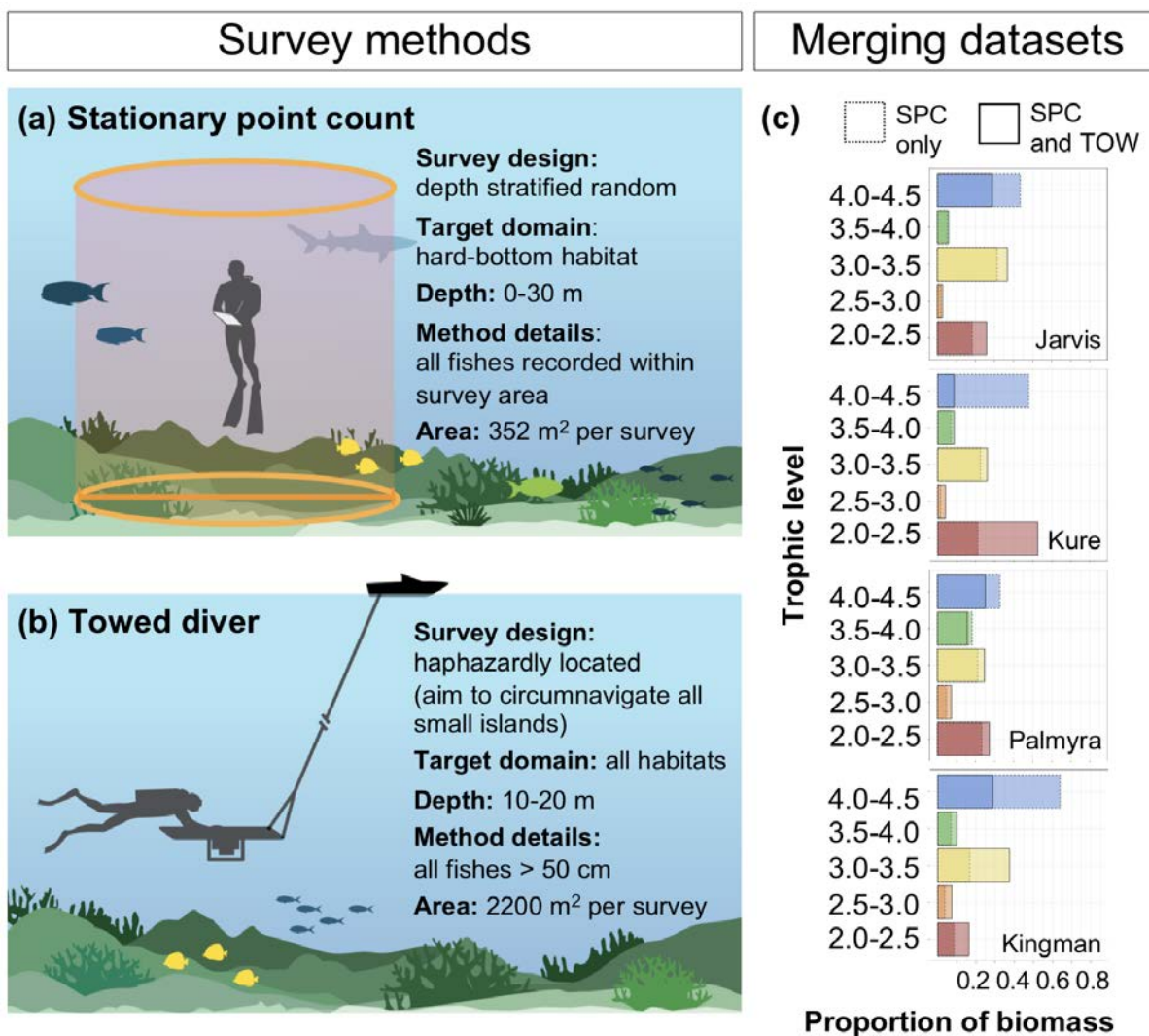


Figure 1. Survey method influences estimated trophic structure of coral reef fish assemblages. Two sampling methods were used to survey fishes a) stationary point count (SPC) and b) towed diver method (tow). c) The SPC is a generalist survey method optimized to capture all fishes within a small (352 m²/survey) area. The d) tow samples large (> 50 cm total length) fish over a large area (2200m²/survey). e) Inverted pyramids at Kure atoll and Jarvis, Kingman and Palmyra, are apparent with the SPC dataset, but not when the SPC and tow are combined (see all WebFigure 2 for all islands).

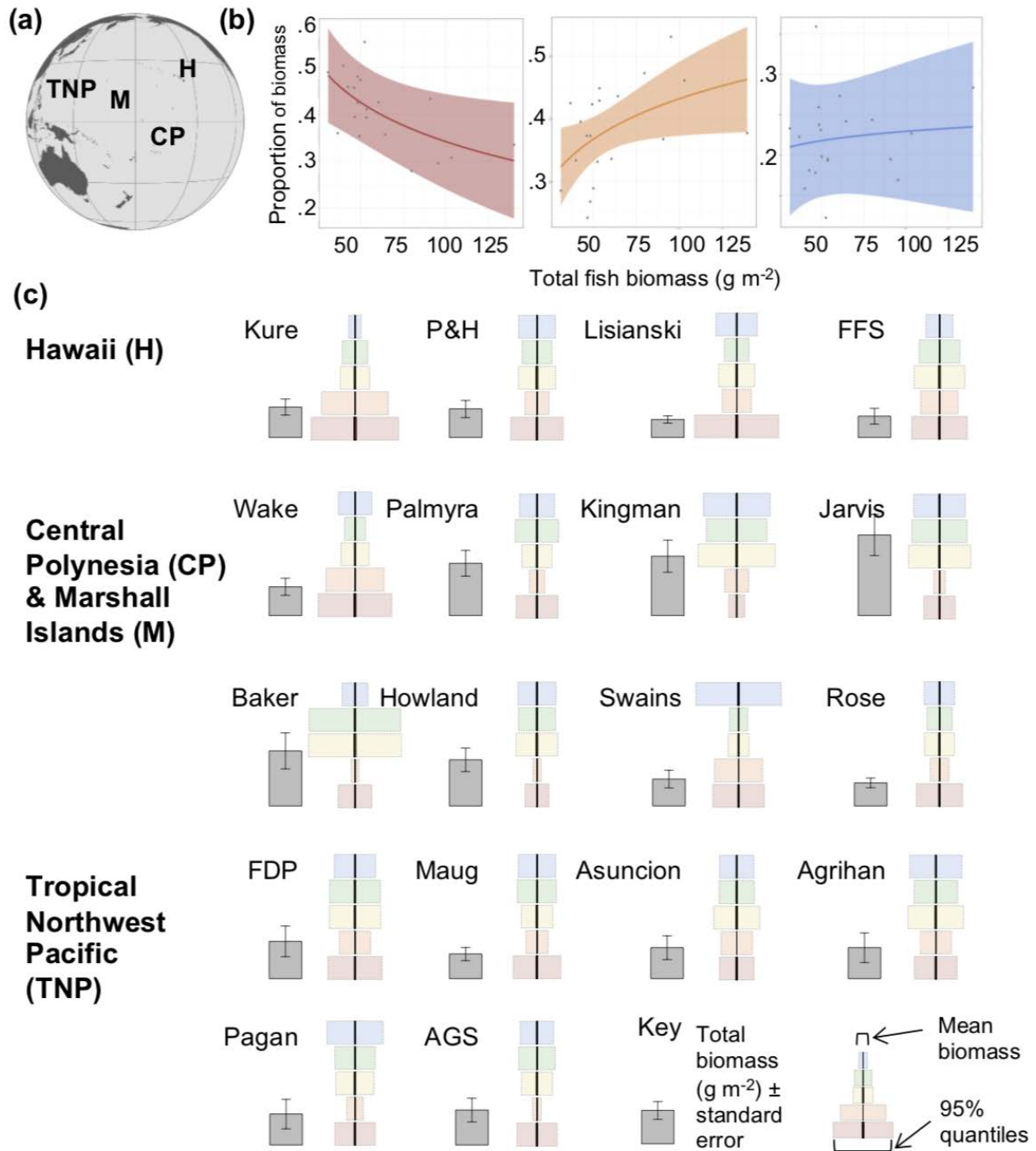


Figure 2. Trophic structure of fish assemblages at coral reef islands. a) Study location b) proportion of biomass per trophic level red: 2-3, orange: 3-4, blue: >4, modelled as a function of total fish biomass g m^{-2} c) Total reef fish biomass (grey) per island ranging from 31 g m^{-2} (Lisianski) to 140 g m^{-2} (Jarvis) and island trophic pyramids (coloured plots) with biomass per trophic level (TL) (proportion of total) (red: 2-2.5, orange: 2.5-3, yellow: 3-3.5, green: 3.5-4, blue: 4-4.5). Mean (dark centre bars in pyramids) and 95% quantiles (coloured transparent bars) were generated from a Monte Carlo simulation. Individual species biomass were drawn from distributions based on mean and standard error from the *in situ* survey data, and species TL designations from FishBase (fixed standard error 0.1).

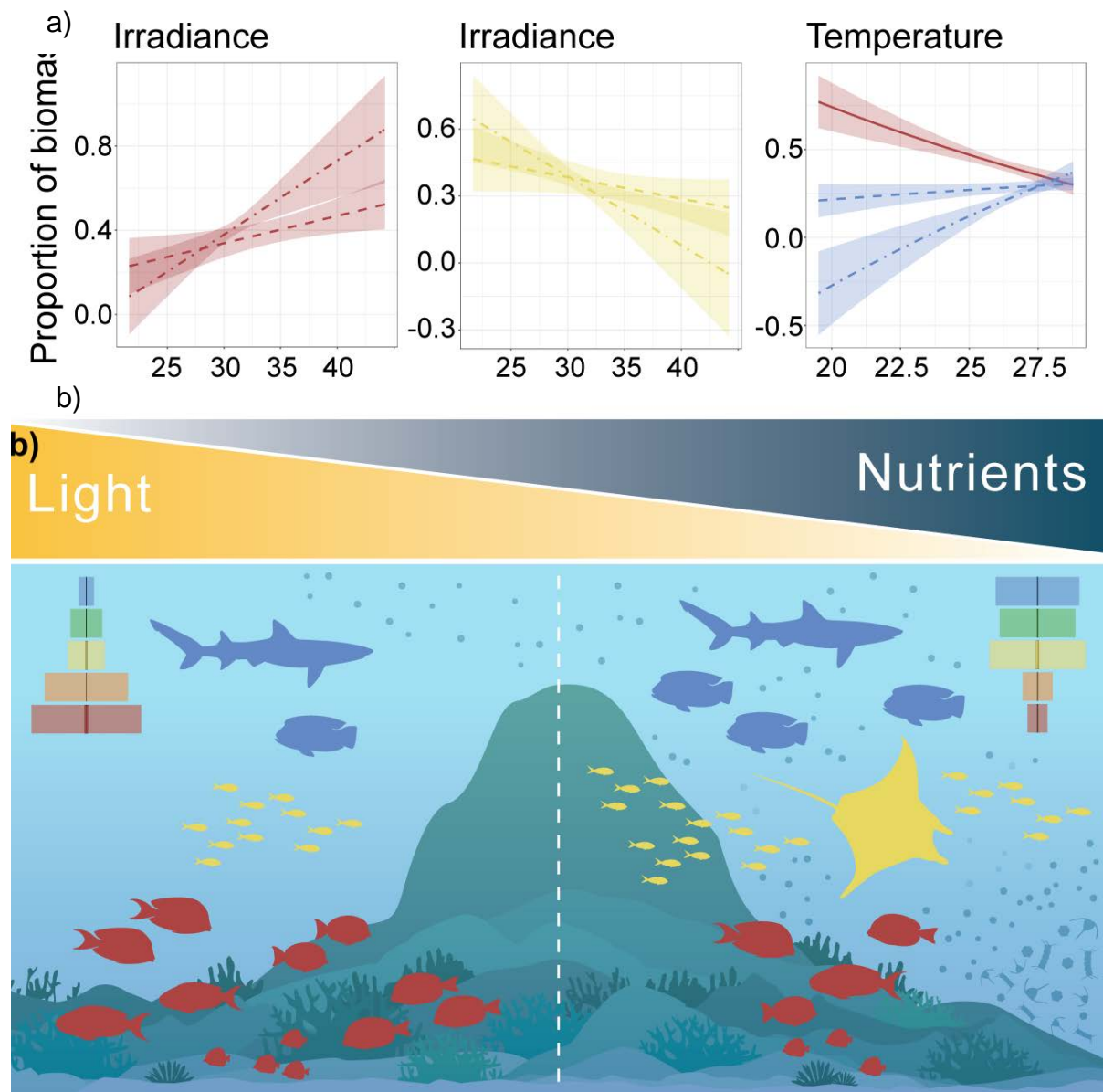


Figure 3. The relationship between irradiance, oceanic primary production and temperature on the trophic structure of coral reef fish assemblages. a) Predicted proportion of biomass and 95% confidence limits for trophic level 2-3 (red), 3-4 (yellow) and > 4 (blue) by Irradiance (Einsteins $m^{-2} d^{-1}$) temperature ($^{\circ}C$) and the interacting effect of oceanic primary productivity (mg m^{-3}) (long dash: high chlorophyll-a, dot-dash: low-chlorophyll-a). b) Conceptual diagram of a bottom-heavy and middle-driven fish assemblage, with fish colour representing trophic levels (red: 2-3, yellow: 3-4, blue: > 4) and inset pyramids from Kure (left) and Kingman (right).

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WebPanel 1. Methods

Fish survey data

We used data collected by the National Oceanic and Atmospheric Administration (NOAA) Pacific Reef Assessment and Monitoring Program (RAMP), a large-scale coral reef ecosystem monitoring program that surveys islands in the tropical U.S. and U.S. affiliated Pacific. The dataset spans 2010-2016, during which coral reef islands and atolls within four regions, the Hawaiian Islands, the Pacific Remote Island Areas, American Samoa and the Mariana Archipelago were visited on a 3-year cycle. Our aim was to assess the trophic structure of minimally impacted coral reef ecosystems, therefore we selected a subset of islands from the NOAA Pacific RAMP dataset, resulting in 21 island replicates. As the surveyed island regions are defined geopolitically, we regrouped them into the Provinces based on the marine ecoregions of the world classification scheme; Tropical Northwest Pacific, Central Polynesia, Marshall Islands and Hawaii (Spalding *et al.* 2007).

The core NOAA Pacific RAMP mandate for monitoring coral reef fish assemblages is to provide information on their status and trends at the island scale across these multiple regions. To achieve this aim, at each island, two survey methods are performed, the stationary point count (Ayotte *et al.* 2015; Heenan *et al.* 2017) and the towed diver technique (Richards *et al.* 2011). The first method, the stationary point count (SPC) was used to survey all observed species within paired 15 m diameter cylinders (total area 352 m² per survey). A random depth stratified survey design was used for inference at the island scale. Divers conducted 'closed' counts i.e. density estimates per taxa were based on the number within the survey unit at single snapshots in time. In contrast, the second method, the towed-diver survey was designed to target large (> 50 cm TL) and roving species within a larger survey area. Divers are towed behind a boat at a target depth of 10-20 m, tow start points are haphazardly selected, and divers collected counts of large fishes ahead of them in a moving 10 × 10 m wide transect (total area per tow ~2200 m²).

From each survey method, we used the diver observations on fish size and abundance to calculate the weight per individual fish (g m⁻²) using length-weight relationships (Kulbicki *et al.* 2005; Froese and Pauly 2016), per survey replicate. A replicate was the average between two SPC paired cylinders and for the tow, an individual tow track. For the SPC, island level species biomass estimates were calculated from the mean values within each depth stratum per island. Biomass estimates were weighted by the total area of each stratum per island and then pooled across years (Heenan *et al.*, 2017; Smith *et al.*, 2011). For the tow, counts were summed over segments and used to calculate an average biomass estimate per tow track based on the length of each individual tow. Island-level species biomass estimates from the tow were calculated as equally weighted means of each tow per island across years.

Sensitivity analysis to integrating the stationary point count and tow diver data

The SPC surveyed a much smaller area than the tow, and this difference in measurement scale influences the encounter and density estimates of species (Panel 1). We addressed this sampling method effect by blending the SPC and tow diver data together. To assess what effect the way in which these data were integrated had on the resultant estimates of biomass per trophic level, we

conducted a sensitivity analysis. Specifically, we merged these data based on a range of criteria value, based on density and encounter rate ratios between methods, and then determined what effect the choice of criteria had on the allocation of biomass across trophic levels (WebTable 2). All stands (70-85%) had more biomass at trophic level 2 and trophic level 3 than 4 whichever way these data were merged, therefore no major differences are seen based on how these data are integrated. The exceptions were the most extreme criteria, where tow was only used when SPC species density estimates were 10-20 times higher and encounter rates 1/10th of that on the tow. In this instance, 33-55% of islands had more biomass at trophic level 2 and 3 than 4. We opted to merge the data based on rule set 1: when a species density estimate was 5 times the density of the tow, use the SPC, and when a species encounter rate was 1/5th times greater on the SPC, use the tow (row 1, WebTable 2). This merged dataset was used for all subsequent analysis.

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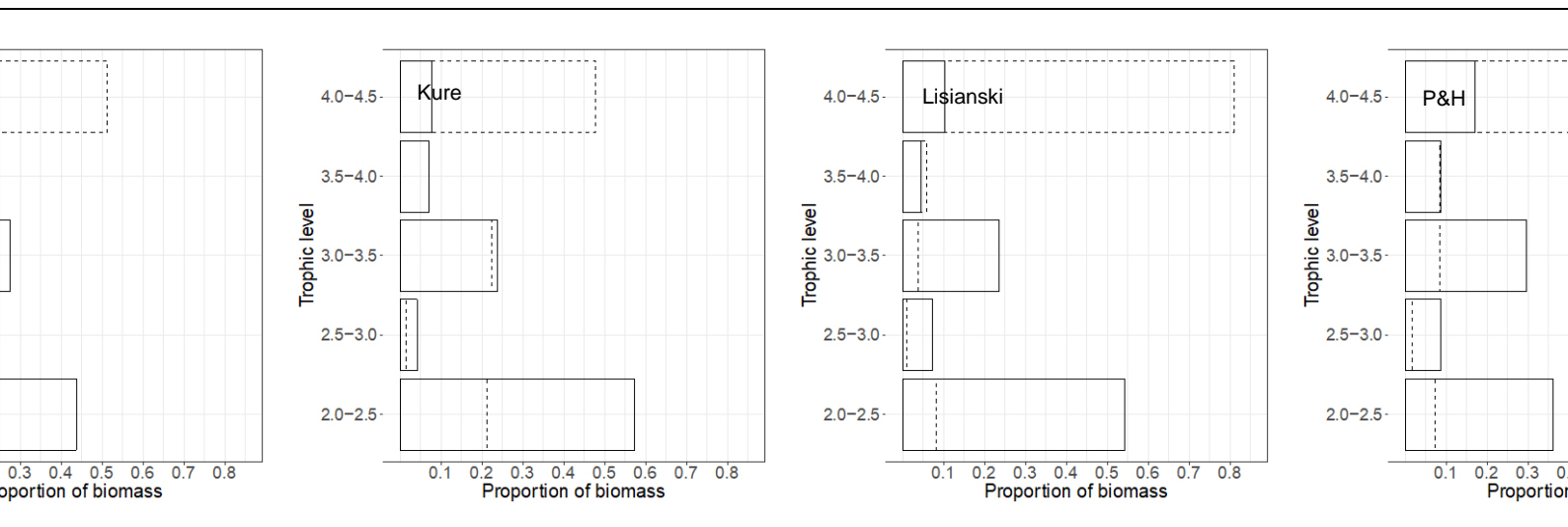
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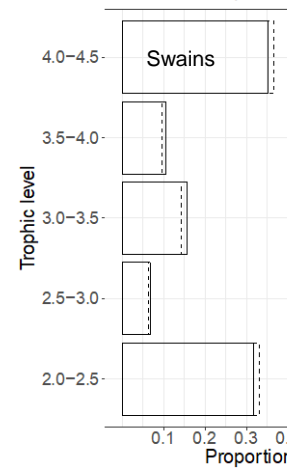
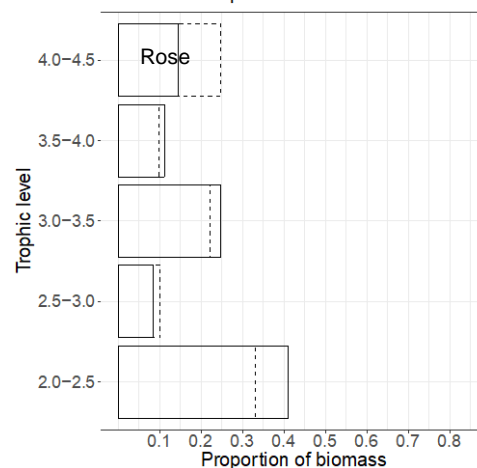
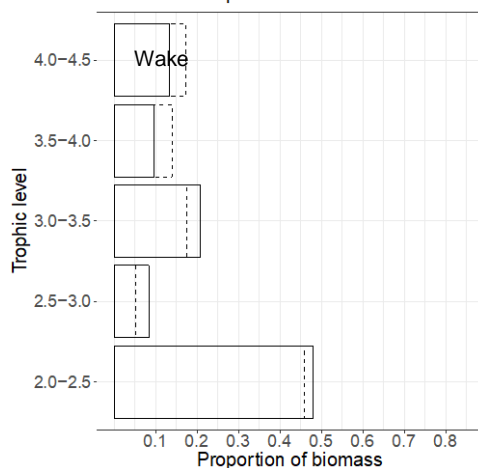
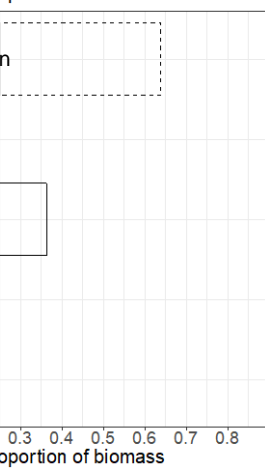
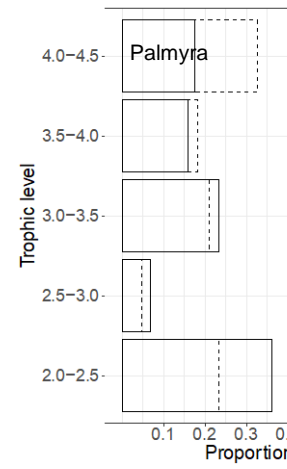
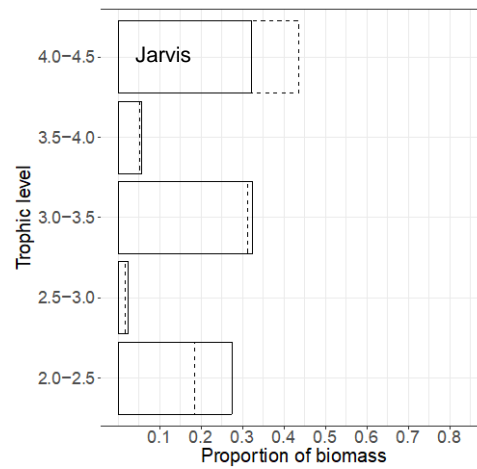
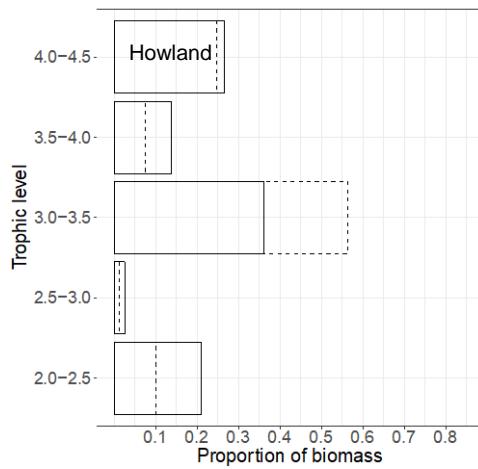
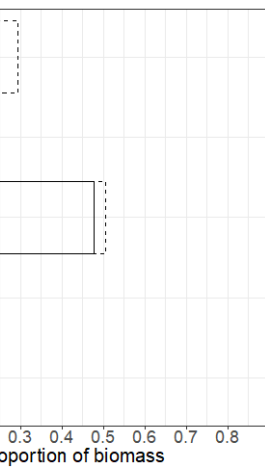
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WebFigure 1. A comparison of the proportion of biomass per different trophic level bin from the stationary point count (SPC) dataset and the integrated SPC and tow dataset. With the SPC dataset (dashed outline), 11 islands appear to be inverted, as compared to none with the blended dataset (black line). FFS = French Frigate Shoals, P&H = Pearl and Hermes, AGS = Alamagan, Guguan, Sarigan.

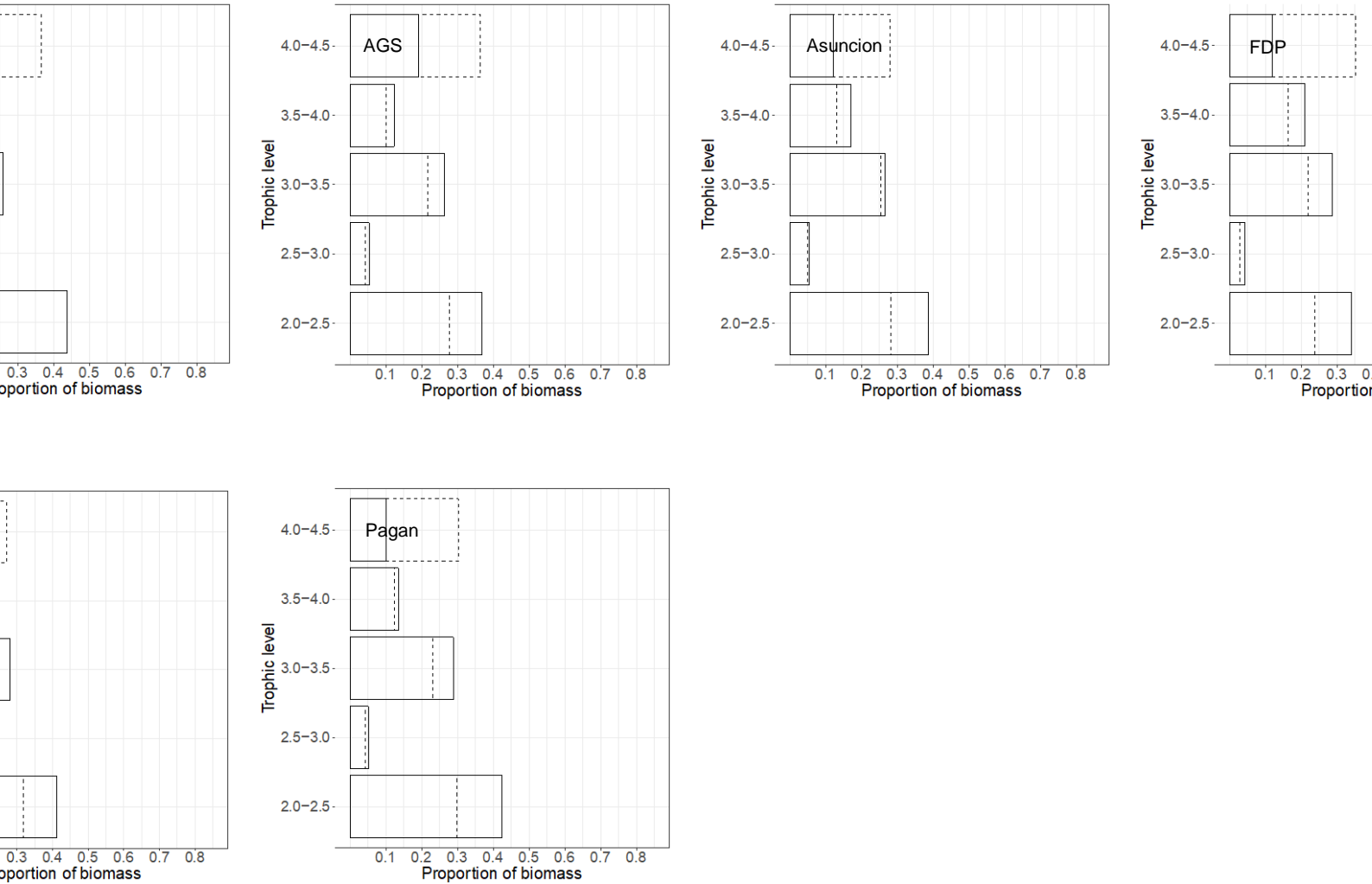
Region: Hawaii



Region: Central Polynesia and Marshall Islands

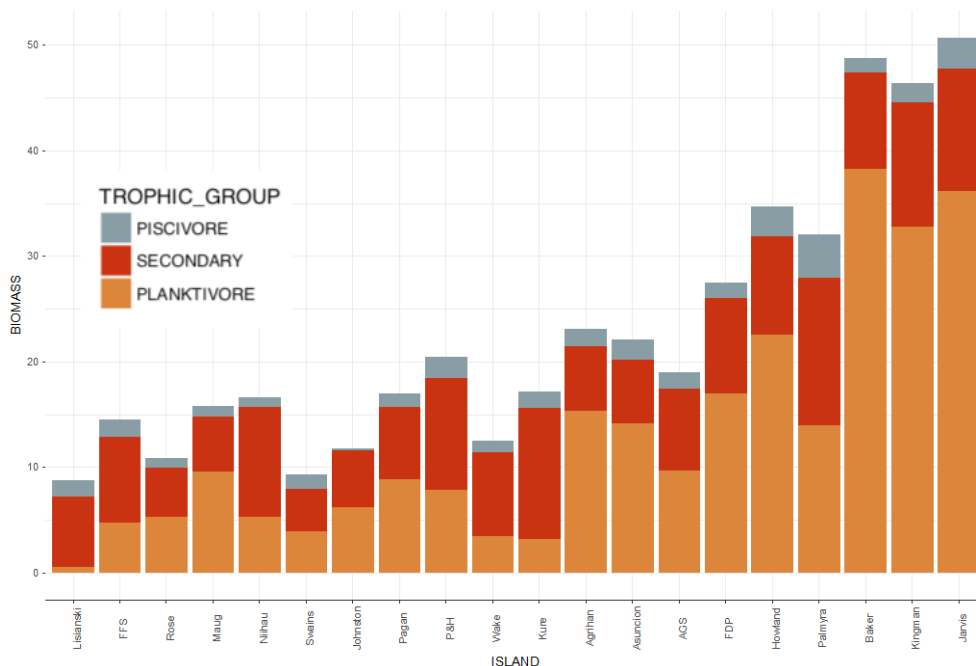
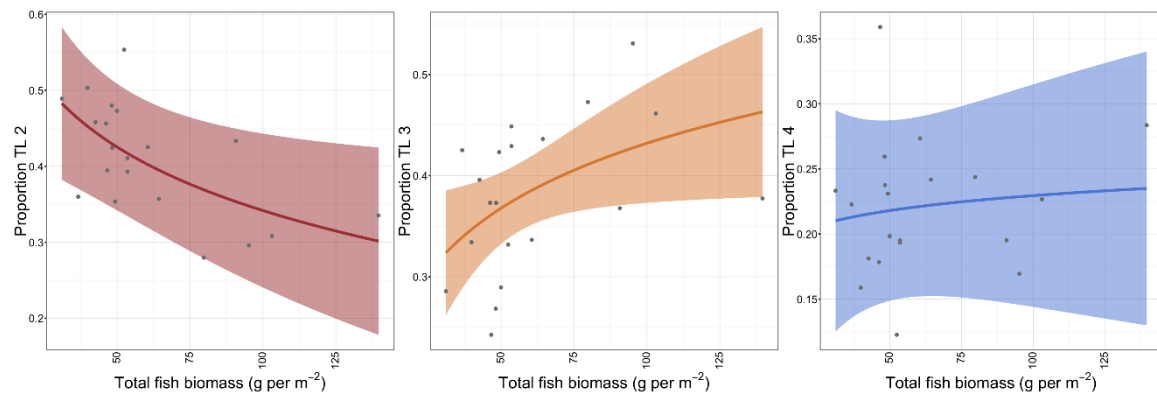


Region: Tropical Northwest Pacific (TNP)



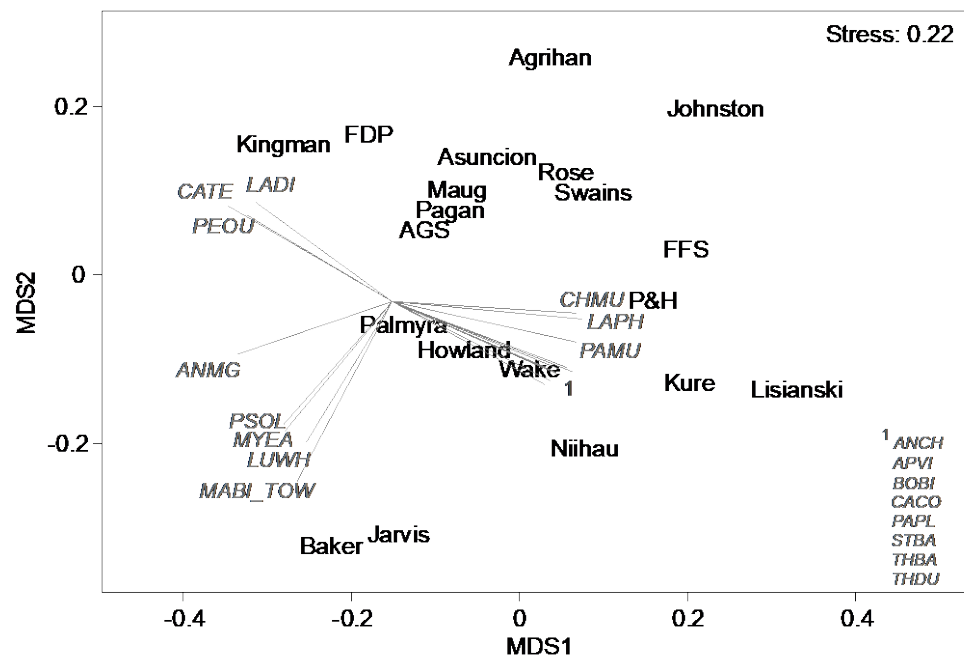
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WebPanel 2 The model fitted relationship between absolute (g m^{-2}) and proportional biomass per trophic level.



contribution of mid-trophic level (trophic level 3 orange) species, in particular planktivorous species (middle graph). The relative contribution of lower trophic levels (trophic level 2 red) was less in islands with increased absolute fish biomass.

The species contributions of mid-trophic level fishes (TL3) to variation in total fish biomass. A metric multi-dimensional scaling based on the Euclidean distance matrix of the proportional contribution of individual species in trophic level 3 was used to identify which species were driving differences in biomass. Islands with the highest total fish biomass, those in Central Polynesia, had increased biomass of mid-trophic level species including the planktivorous rays *Manta* spp. and anthias (*Luzonichthys whitleyi* and *Pseudanthias olivaceus*), small wrasses *Anampses meleagrides* and *Labroides didimatus*, sweepers *Pempheris oualensis* and fusilier *Caesio teres*.



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WebTable 2. A sensitivity test to integrate the stationary point count and tow diver data.

We tested a range of criteria for merging the tow and the SPC datasets together. These criteria were based on fish species density and encounter rates within each dataset. After each time the data were merged together based on the different criteria (rows), we inspected the outcome this had on the total amount of biomass in each trophic level. This is summarized as the percentage of islands with more biomass at trophic level 2 ($2 < 3$) and 3 ($3 < 4$) than trophic level 4. The islands listed are those with TL2 biomass $>$ TL4. Variations of the data merging rules, e.g. twice the density and $1/5^{\text{th}}$ of the encounter rate, or five times the density and $1/10^{\text{th}}$ of the encounter rate all resulted in species records being used from the tow dataset, which is equivalent to row 1 and 2 so are not displayed here.

| Data merging criteria | | Outcome | | |
|---|---|-------------------------------------|------------------------------------|--|
| When a species density estimate is n times greater on SPC, tow data is used | When a species encounter rate is n times greater on SPC, tow data is used | % Islands* with TL2 biomass $>$ TL4 | % Islands with TL3 biomass $<$ TL4 | Islands |
| 5 | $1/5^{\text{th}}$ | 72 | 0 | Baker, Howland, Jarvis, Kingman, Swains |
| 10 | $1/5^{\text{th}}$ | 72 | 0 | Baker, Howland, Jarvis, Kingman, Swains |
| 20 | $1/5^{\text{th}}$ | 55 | 0 | Agrihan, AGS, Baker, FDP, Howland, Jarvis, Kingman, Swains |
| 10 | $1/10^{\text{th}}$ | 33 | 0 | Agrihan, AGS, Baker, FDP, FFS, Howland, Jarvis, Kingman, Lisianski, P&H, Palmyra, Swains |
| 20 | $1/10^{\text{th}}$ | 50 | 0 | Agrihan, AGS, Baker, FDP, Howland, Jarvis, Kingman, Palmyra, Swains |

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WebPanel 3 Biophysical drivers in coral reef fish trophic structure - modelling procedure

For each trophic level, proportional and absolute biomass (termed herein biomass response metrics) was modelled as function of the three biophysical explanatory factors: 1) irradiance (IRR); 2) oceanic primary production (CHL) and; 3) sea-surface temperature (SST). Island level climatologies of each biophysical parameter were taken from Gove *et al.* (2013), specifically the mean estimates of chlorophyll-*a* (mg m^{-3}) and irradiance ($\text{E m}^{-2} \text{d}^{-1}$) and lower climatological mean of sea-surface temperature ($^{\circ} \text{Celsius}$). The biophysical predictors were inspected for co-linearity (variance inflation factors were < 5 and correlation $R^2 < 0.75$) and normalized (centered and scaled by their standard deviations).

The model fitting process was as follows, the maximal model with and without a random effect of Province (Tropical Northwest Pacific, Central Polynesia, Marshall Islands and Hawaii) was fitted, and the Akaike's Information Criterion (AIC) weight used to identify whether a model with a random intercept for Province better fit the data than a model with no random term.

All proportional biomass models, as well as absolute biomass of trophic level 2 and 4 had a higher conditional probability with no random effect. The proportion of biomass per trophic level and the absolute biomass for trophic level 4 were then fitted as generalized linear models (glm), while the absolute biomass of trophic level 3 was fitted as a mixed effects model (glmm). Absolute trophic level 4 biomass was log-transformed as these data were right skewed. Once we established whether the biomass metrics would be fitted via a glmm or glm, we took the following model selection steps. For each biomass response metric we ran all possible combinations of the biophysical factors with and without interaction terms along with a null model (for the mixed effects models this contained only the random effect of Province). For each biomass response metric model set, the AIC weight corrected for small sample size (AICc), was used to assess the conditional probability of each model and the strength of association between the biomass metrics and the biophysical drivers (Anderson 2008). The effect of the predictors terms were then visualized based on a predicted dataset generated from the best candidate model. For each trophic level model, values of the response were estimated along the range of values of the predictor of interest, after setting the other predictor terms to their median value. This was done via the visreg package in R (Breheny and Burchett 2017).

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WebTable 1. A comparison of the density estimates (abundance and biomass (g) per ha) and encounter rates (number of individuals per hectare) of species recorded on both the stationary point count (SPC) and tow (TOW) surveys. This comparison was made for individuals > 50 cm total length on both method over ~ 1000 surveys of each method. TL = trophic level, LMAX = maximum recorded species length, Count = total number recorded (over a total area sampled of ~2130 Ha on the tow and 37 Ha on the SPC), abundance per Ha (Abund/Ha), encounter rate per survey (Encnt/Surv), biomass of fish (g/ha) and encounter rate (Abundance/ha).

| T L | Common family | Species | LMAX | TOW | | | | SPC | | | | Ratios (SPC:TOW) | | |
|--------|---------------|---------------------------------|---------|----------|----------|------------|-------------|---------|----------|------------|--------------|------------------|------------|-----------|
| | | | | Count | Abund/Ha | Encnt/Surv | g/Ha | Count | Abund/Ha | Encnt/Surv | g/Ha | Abund/Ha | Encnt/Surv | g/Ha |
| 2 | Parrotfish | <i>Scarus frenatus</i> | 47 | 8 | 0.00 | 0.01 | 12.8 6 | 1 | 0.03 | 0.00 | 93.70 | 7.28 | 0.12 | 7.2 8 |
| 2 | Parrotfish | <i>Scarus xanthopleura</i> | 55 | 28 | 0.01 | 0.03 | 34.1 3 | 3 | 0.08 | 0.00 | 357.4 1 | 6.24 | 0.10 | 10. 47 |
| 2 | Parrotfish | <i>Chlorurus frontalis</i> | 50 | 45 | 0.02 | 0.05 | 70.0 6 | 3 | 0.08 | 0.00 | 489.9 2 | 3.88 | 0.06 | 6.9 9 |
| 2 | Parrotfish | <i>Scarus rubroviolaceus</i> | 70 | 18 28 | 0.86 | 1.86 | 2871 .11 | 11 1 | 3.04 | 0.11 | 1402 9.57 | 3.54 | 0.06 | 4.8 9 |
| 2 | Parrotfish | <i>Cetoscarus ocellatus</i> | 90 | 90 | 0.04 | 0.09 | 115. 08 | 4 | 0.11 | 0.00 | 411.4 6 | 2.59 | 0.04 | 3.5 8 |
| 2 | Parrotfish | <i>Chlorurus perspicillatus</i> | 62 | 45 4 | 0.21 | 0.46 | 597. 53 | 16 | 0.44 | 0.02 | 2124. 48 | 2.05 | 0.03 | 3.5 6 |
| 2 | Parrotfish | <i>Hipposcarus longiceps</i> | 60 | 60 | 0.03 | 0.06 | 79.6 6 | 2 | 0.05 | 0.00 | 152.3 6 | 1.94 | 0.03 | 1.9 1 |
| 2 | Parrotfish | <i>Scarus altipinnis</i> | 60 | 11 7 | 0.05 | 0.12 | 155. 68 | 2 | 0.05 | 0.00 | 155.0 2 | 1.00 | 0.02 | 1.0 0 |
| 2 | Surgeonfish | <i>Naso tonganus</i> | 63 | 71 | 0.03 | 0.07 | 145. 60 | 13 | 0.36 | 0.01 | 3043. 19 | 10.67 | 0.17 | 20. 90 |
| 2 | Surgeonfish | <i>Naso unicornis</i> | 70 | 21 4 | 0.10 | 0.22 | 244. 17 | 18 | 0.49 | 0.02 | 1037. 01 | 4.90 | 0.08 | 4.2 5 |
| 2 4 | Surgeonfish | <i>Acanthurus xanthopterus</i> | 65 | 29 | 0.01 | 0.03 | 28.2 6 | 6 | 0.16 | 0.01 | 382.2 5 | 12.06 | 0.20 | 13. 53 |
| 2 6 | Surgeonfish | <i>Naso annulatus</i> | 10 0 | 36 | 0.02 | 0.04 | 70.0 6 | 15 | 0.41 | 0.01 | 1508. 91 | 24.28 | 0.40 | 21. 54 |
| 2 7 | Parrotfish | <i>Chlorurus microrhinos</i> | 80 | 11 61 | 0.55 | 1.18 | 1423 .89 | 12 5 | 3.42 | 0.12 | 1288 3.92 | 6.27 | 0.10 | 9.0 5 |
| 2 7 | Surgeonfish | <i>Naso brevirostris</i> | 60 | 10 | 0.00 | 0.01 | 18.0 6 | 5 | 0.14 | 0.00 | 424.0 8 | 29.13 | 0.48 | 23. 48 |
| 2 7 | Surgeonfish | <i>Naso brachycentron</i> | 90 | 21 | 0.01 | 0.02 | 39.5 2 | 3 | 0.08 | 0.00 | 1008. 58 | 8.32 | 0.14 | 25. 52 |

| | | | | | | | | | | | | | | |
|---|-------------|---------------------------------------|-----|------|------|------|----------|-----|------|------|-----------|--------|------|--------|
| 2 | Triggerfish | <i>Pseudobalistes flavimarginatus</i> | 60 | 91 | 0.04 | 0.09 | 167.63 | 24 | 0.66 | 0.02 | 2941.57 | 15.37 | 0.25 | 17.55 |
| 2 | Filefish | <i>Aluterus scriptus</i> | 76 | 77 | 0.04 | 0.08 | 13.29 | 9 | 0.25 | 0.01 | 123.67 | 6.81 | 0.11 | 9.31 |
| 3 | Emperor | <i>Monotaxis grandoculis</i> | 63 | 90 | 0.04 | 0.09 | 98.08 | 35 | 0.96 | 0.03 | 2527.58 | 22.66 | 0.37 | 25.77 |
| 3 | Ray | <i>Aetobatus narinari</i> | 350 | 153 | 0.07 | 0.16 | 1094.54 | 8 | 0.22 | 0.01 | 5678.86 | 3.05 | 0.05 | 5.19 |
| 3 | Surgeonfish | <i>Naso hexacanthus</i> | 75 | 1034 | 0.49 | 1.05 | 1191.08 | 342 | 9.36 | 0.33 | 2431.94 | 19.27 | 0.32 | 20.41 |
| 3 | Triggerfish | <i>Balistoides viridescens</i> | 75 | 93 | 0.04 | 0.09 | 187.03 | 7 | 0.19 | 0.01 | 1434.38 | 4.39 | 0.07 | 7.67 |
| 3 | Surgeonfish | <i>Naso vlamingii</i> | 60 | 252 | 0.12 | 0.26 | 353.22 | 41 | 1.12 | 0.04 | 3935.40 | 9.48 | 0.15 | 11.14 |
| 3 | Wrasse | <i>Bodianus bilunulatus</i> | 55 | 10 | 0.00 | 0.01 | 8.57 | 6 | 0.16 | 0.01 | 521.41 | 34.96 | 0.57 | 60.84 |
| 3 | Wrasse | <i>Coris aygula</i> | 120 | 46 | 0.02 | 0.05 | 50.76 | 10 | 0.27 | 0.01 | 1085.16 | 12.67 | 0.21 | 21.38 |
| 3 | Knifejaw | <i>Oplegnathus punctatus</i> | 86 | 96 | 0.05 | 0.10 | 173.80 | 29 | 0.79 | 0.03 | 2003.22 | 17.60 | 0.29 | 11.53 |
| 3 | Soldierfish | <i>Sargocentron spiniferum</i> | 52 | 1 | 0.00 | 0.00 | 1.15 | 1 | 0.03 | 0.00 | 66.90 | 58.27 | 0.95 | 58.27 |
| 3 | Ray | <i>Manta birostris</i> | 800 | 120 | 0.06 | 0.12 | 12612.50 | 25 | 0.68 | 0.02 | 251974.19 | 12.14 | 0.20 | 19.98 |
| 3 | Jack | <i>Elagatis bipinnulata</i> | 180 | 649 | 0.30 | 0.66 | 217.35 | 280 | 7.66 | 0.27 | 6700.31 | 25.14 | 0.41 | 30.83 |
| 3 | Grunt | <i>Plectorhinchus gibbosus</i> | 75 | 28 | 0.01 | 0.03 | 55.37 | 2 | 0.05 | 0.00 | 367.00 | 4.16 | 0.07 | 6.63 |
| 3 | Emperor | <i>Lethrinus xanthurus</i> | 62 | 2 | 0.00 | 0.00 | 1.98 | 10 | 0.27 | 0.01 | 655.84 | 291.34 | 4.76 | 331.04 |
| 3 | Emperor | <i>Lethrinus olivaceus</i> | 100 | 24 | 0.01 | 0.02 | 32.41 | 27 | 0.74 | 0.03 | 2432.09 | 65.55 | 1.07 | 75.04 |
| 3 | Grunt | <i>Plectorhinchus picus</i> | 85 | 60 | 0.03 | 0.06 | 73.13 | 1 | 0.03 | 0.00 | 131.94 | 0.97 | 0.02 | 1.80 |
| 3 | Grouper | <i>Epinephelus polyphemus</i> | 75 | 12 | 0.01 | 0.01 | 16.30 | 22 | 0.60 | 0.02 | 1962.80 | 106.82 | 1.75 | 120.42 |
| 3 | Jack | <i>Pseudocaranx dentex</i> | 122 | 54 | 0.03 | 0.05 | 100.87 | 1 | 0.03 | 0.00 | 186.70 | 1.08 | 0.02 | 1.85 |
| 3 | Shark | <i>Carcharhinus melanopterus</i> | 200 | 214 | 0.10 | 0.22 | 1135.24 | 70 | 1.92 | 0.07 | 26634.70 | 19.06 | 0.31 | 23.46 |

| | | | | | | | | | | | | | | |
|---|-------------|-------------------------------|----|----|------|------|------|----|-------|------|-------|-------|------|-----|
| 3 | | | | | | | | | | | | | | |
| . | | <i>Plectorhinchus</i> | | | | | | | | | 434.1 | | | 57. |
| 9 | Grunt | <i>vittatus</i> | 85 | 8 | 0.00 | 0.01 | 7.60 | 3 | 0.08 | 0.00 | 3 | 21.85 | 0.36 | 09 |
| | | | 11 | 62 | | | 1354 | 36 | | | 3673 | | | 27. |
| 4 | Snapper | <i>Aprion virescens</i> | 2 | 5 | 0.29 | 0.63 | .04 | 2 | 9.91 | 0.35 | 4.62 | 33.75 | 0.55 | 13 |
| | | | | 22 | | | 206. | | | | 1973. | | | 9.5 |
| 4 | Snapper | <i>Macolor macularis</i> | 60 | 2 | 0.10 | 0.23 | 37 | 21 | 0.57 | 0.02 | 63 | 5.51 | 0.09 | 6 |
| | | | | 42 | | | 404. | | | | 3627. | | | 8.9 |
| 4 | Snapper | <i>Macolor niger</i> | 75 | 2 | 0.20 | 0.43 | 00 | 39 | 1.07 | 0.04 | 86 | 5.38 | 0.09 | 8 |
| | | | 22 | 19 | | | 1831 | | | | 2182 | | | 11. |
| 4 | Wrasse | <i>Cheilinus undulatus</i> | 9 | 0 | 0.09 | 0.19 | .35 | 22 | 0.60 | 0.02 | 9.79 | 6.75 | 0.11 | 92 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Epinephelus</i> | | | | | | | | | 134.0 | | | 28. |
| 1 | Grouper | <i>tauvina</i> | 75 | 5 | 0.00 | 0.01 | 4.67 | 3 | 0.08 | 0.00 | 9 | 34.96 | 0.57 | 68 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Plectropomus</i> | 12 | | | | 153. | | | | 2313. | | | 15. |
| 1 | Grouper | <i>laevis</i> | 5 | 41 | 0.02 | 0.04 | 95 | 13 | 0.36 | 0.01 | 31 | 18.48 | 0.30 | 03 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Carcharhinus</i> | 24 | 19 | | | 1240 | 62 | | | 3130 | | | 25. |
| 1 | Shark | <i>amblyrhynchos</i> | 0 | 06 | 0.90 | 1.94 | 0.48 | 7 | 17.16 | 0.61 | 31.16 | 19.17 | 0.31 | 24 |
| | | | | | | | | | | | | | | |
| 4 | | | 40 | | | | 538. | | | | 3660. | | | 6.8 |
| 1 | Shark | <i>Sphyrna lewini</i> | 0 | 14 | 0.01 | 0.01 | 63 | 2 | 0.05 | 0.00 | 08 | 8.32 | 0.14 | 0 |
| | | | | | | | | | | | | | | |
| 4 | | | | | | | 10.2 | | | | 155.5 | | | 15. |
| 1 | Snapper | <i>Aphareus furca</i> | 70 | 16 | 0.01 | 0.02 | 7 | 4 | 0.11 | 0.00 | 5 | 14.57 | 0.24 | 15 |
| | | | | | | | | | | | | | | |
| 4 | | | | 36 | | | 5498 | 85 | | | 8865 | | | 16. |
| 1 | Snapper | <i>Lutjanus bohar</i> | 90 | 95 | 1.74 | 3.75 | .53 | 7 | 23.45 | 0.83 | 7.43 | 13.51 | 0.22 | 12 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Parupeneus</i> | | | | | | | | | | | | 7.2 |
| 2 | Goatfish | <i>cyclostomus</i> | 50 | 12 | 0.01 | 0.01 | 8.73 | 2 | 0.05 | 0.00 | 63.62 | 9.71 | 0.16 | 8 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Gracila</i> | | | | | | | | | 272.9 | | | 149 |
| 2 | Grouper | <i>albomarginata</i> | 50 | 2 | 0.00 | 0.00 | 1.83 | 3 | 0.08 | 0.00 | 8 | 87.40 | 1.43 | .24 |
| | | | | | | | | | | | | | | |
| 4 | | | 16 | 80 | | | 3886 | 74 | | | 2121 | | | 54. |
| 2 | Jack | <i>Caranx ignobilis</i> | 5 | 1 | 0.38 | 0.81 | .63 | 2 | 20.30 | 0.72 | 06.07 | 53.98 | 0.88 | 57 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Carcharhinus</i> | 37 | | | | 623. | | | | 3689 | | | 59. |
| 2 | Shark | <i>galapagensis</i> | 0 | 87 | 0.04 | 0.09 | 73 | 51 | 1.40 | 0.05 | 5.81 | 34.16 | 0.56 | 15 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Triacnodon</i> | 21 | 47 | | | 1835 | 13 | | | 3690 | | | 20. |
| 2 | Shark | <i>obesus</i> | 3 | 2 | 0.22 | 0.48 | .30 | 9 | 3.80 | 0.13 | 8.31 | 17.16 | 0.28 | 11 |
| | | | | | | | | | | | | | | |
| 4 | | | 18 | | | | 143. | | | | 628.2 | | | 4.3 |
| 2 | Ray | <i>Taeniura meyeni</i> | 0 | 38 | 0.02 | 0.04 | 16 | 2 | 0.05 | 0.00 | 8 | 3.07 | 0.05 | 9 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Aulostomus</i> | | 19 | | | 30.1 | | | | 422.1 | | | 14. |
| 2 | Trumpetfish | <i>chinensis</i> | 80 | 1 | 0.09 | 0.19 | 4 | 30 | 0.82 | 0.03 | 2 | 9.15 | 0.15 | 01 |
| | | | | | | | | | | | | | | |
| 4 | | | | 22 | | | 198. | | | | 3523. | | | 17. |
| 3 | Grouper | <i>Variola louti</i> | 83 | 5 | 0.11 | 0.23 | 01 | 59 | 1.61 | 0.06 | 03 | 15.28 | 0.25 | 79 |
| | | | | | | | | | | | | | | |
| 4 | | <i>Lutjanus</i> | | | | | 18.6 | | | | 1138. | | | 61. |
| 3 | Snapper | <i>monostigma</i> | 60 | 20 | 0.01 | 0.02 | 1 | 14 | 0.38 | 0.01 | 12 | 40.79 | 0.67 | 17 |
| | | | | | | | | | | | | | | |
| 4 | | | | | | | 81.9 | | | | 494.7 | | | 6.0 |
| 3 | Cornetfish | <i>Fistularia commersonii</i> | 16 | 35 | | 0.36 | 3 | 40 | 1.09 | 0.04 | 7 | 6.57 | 0.11 | 4 |

| | | | | | | | | | | | | | | | |
|----|---|-----------|---------------------------------|-----|------|------|------|---------|-----|-------|------|----------|-------|------|-------|
| 45 | . | Barracuda | <i>Sphyaena barracuda</i> | 200 | 66 | 0.03 | 0.07 | 124.69 | 53 | 1.45 | 0.05 | 6009.11 | 46.79 | 0.76 | 48.19 |
| 45 | . | Barracuda | <i>Sphyaena helleri</i> | 80 | 697 | 0.33 | 0.71 | 199.65 | 130 | 3.56 | 0.13 | 4939.26 | 10.87 | 0.18 | 24.74 |
| 45 | . | Barracuda | <i>Sphyaena qenie</i> | 170 | 3734 | 1.75 | 3.79 | 4312.22 | 428 | 11.71 | 0.41 | 28164.30 | 6.68 | 0.11 | 6.53 |
| 45 | . | Grouper | <i>Cephalopholis argus</i> | 60 | 58 | 0.03 | 0.06 | 66.19 | 24 | 0.66 | 0.02 | 1821.26 | 24.11 | 0.39 | 27.52 |
| 45 | . | Jack | <i>Caranx melampygus</i> | 117 | 566 | 0.27 | 0.57 | 1046.22 | 308 | 8.43 | 0.30 | 27606.10 | 31.71 | 0.52 | 26.39 |
| 45 | . | Jack | <i>Seriola dumerili</i> | 190 | 43 | 0.02 | 0.04 | 158.88 | 19 | 0.52 | 0.02 | 5082.18 | 25.75 | 0.42 | 31.99 |
| 45 | . | Jack | <i>Carangoides orthogrammus</i> | 70 | 84 | 0.04 | 0.09 | 73.45 | 11 | 0.30 | 0.01 | 701.93 | 7.63 | 0.12 | 9.56 |
| 45 | . | Jack | <i>Scomberoides lysan</i> | 70 | 36 | 0.02 | 0.04 | 15.92 | 3 | 0.08 | 0.00 | 60.92 | 4.86 | 0.08 | 3.83 |
| 45 | . | Jack | <i>Caranx lugubris</i> | 100 | 502 | 0.24 | 0.51 | 512.88 | 26 | 0.71 | 0.03 | 1975.54 | 3.02 | 0.05 | 3.85 |
| 45 | . | Jack | <i>Caranx sexfasciatus</i> | 100 | 2539 | 1.19 | 2.58 | 3367.46 | 37 | 1.01 | 0.04 | 3796.46 | 0.85 | 0.01 | 1.13 |

A Heenan *et al.* - Supporting Information

WebPanel 4 Biophysical drivers in coral reef fish trophic structure - modelling outputs

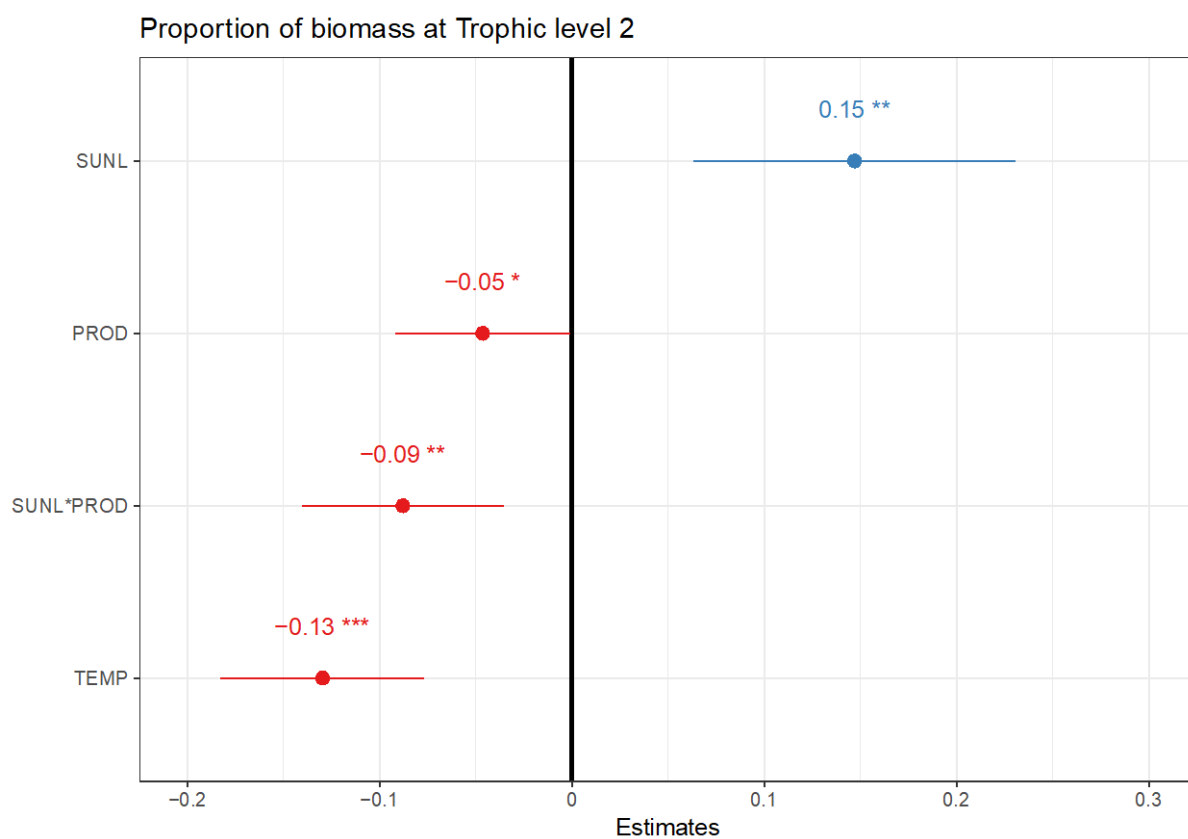
Summary of the model outputs for each trophic level and each biomass metric (proportion and absolute). A table of the conditional probability of each model from the model fitting process is presented. SUNL = Irradiance ($\text{Einsteins m}^{-2} \text{ d}^{-1}$), PROD = chlorophyll a (mg m^{-3}), TEMP = sea surface temperature ($^{\circ} \text{Celsius}$), k = the number of estimated parameters, ΔAICc = delta AICc, LogL = log likelihood and w = AICc weights corrected for small sample size. With the model entries '+' for additive effects and '*' for interaction terms.

Trophic level 2 proportional biomass model performance

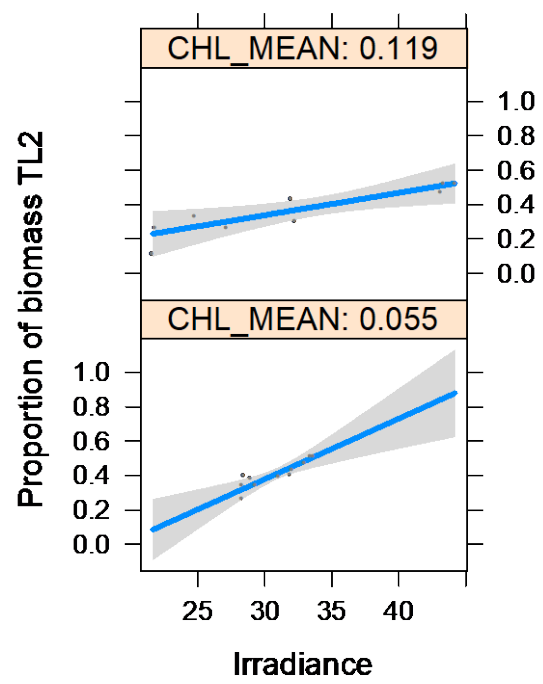
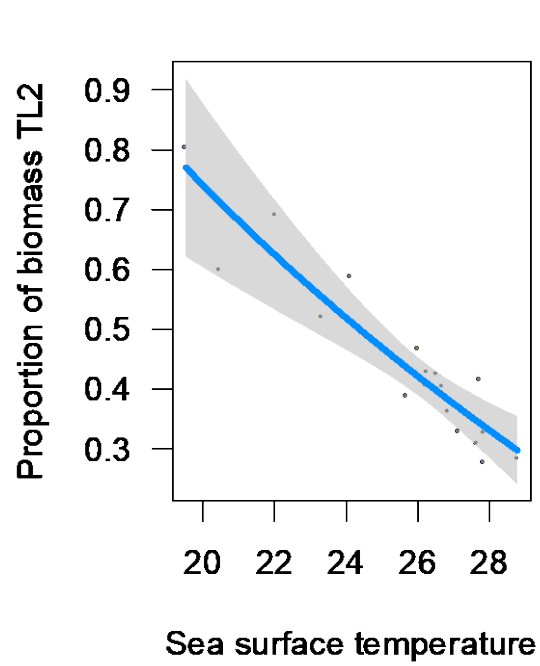
| Model | K | AICc | d | w | LogL |
|---------------------------|----------|---------------|-------------|-------------|--------------|
| SUNL * PROD + TEMP | 6 | -47.39 | 0.00 | 0.94 | 32.92 |
| PROD + TEMP | 4 | -40.90 | 6.49 | 0.04 | 25.78 |
| SUNL + PROD + TEMP | 5 | -39.25 | 8.14 | 0.02 | 26.77 |
| SUNL * TEMP + PROD | 6 | -36.21 | 11.18 | 0.00 | 27.34 |
| SUNL + TEMP * PROD | 6 | -35.07 | 12.32 | 0.00 | 26.77 |
| SUNL | 3 | -34.78 | 12.61 | 0.00 | 21.14 |
| SUNL * TEMP * PROD | 9 | -33.99 | 13.40 | 0.00 | 34.99 |
| SUNL + TEMP | 4 | -33.69 | 13.69 | 0.00 | 22.18 |
| SUNL + PROD | 4 | -31.83 | 15.56 | 0.00 | 21.25 |
| PROD | 3 | -28.57 | 18.82 | 0.00 | 18.03 |
| NULL | 2 | -27.53 | 19.86 | 0.00 | 16.12 |

Trophic level 2 proportional biomass top candidate model

Effect size plot from highest ranked linear model (F statistic (df 4,15): 16.39, $p < 0.001$), with an adjusted R^2 of 0.76. Dots represent mean effect sizes, lines are the 95% confidence limit. Limits that span the vertical line indicate no effect.



Trophic level 2 – proportional biomass – highest ranked model plots. Irradiance ($\text{Einsteins m}^{-2} \text{ d}^{-1}$), CHL_MEAN = chlorophyll a (mg m^{-3}), sea surface temperature ($^{\circ} \text{Celsius}$)



Trophic level 2 absolute biomass model performance

| Model | K | AICc | d | w | LogL |
|--------------------|----------|---------------|-------------|-------------|---------------|
| PROD | 4 | 124.09 | 0.00 | 0.22 | -56.62 |
| SUNL + PROD | 5 | 125.11 | 1.02 | 0.13 | -55.25 |
| PROD + TEMP | 5 | 125.41 | 1.32 | 0.11 | -55.40 |
| SUNL + PROD + TEMP | 6 | 125.58 | 1.49 | 0.11 | -53.29 |
| SUNL * PROD + TEMP | 7 | 125.81 | 1.72 | 0.09 | -50.81 |
| SUNL + TEMP * PROD | 7 | 125.87 | 1.78 | 0.09 | -50.84 |
| SUNL + TEMP | 5 | 126.53 | 2.44 | 0.07 | -55.96 |
| SUNL * TEMP + PROD | 7 | 126.72 | 2.63 | 0.06 | -51.27 |
| SUNL * TEMP * PROD | 10 | 127.76 | 3.67 | 0.04 | -40.13 |
| SUNL | 4 | 128.03 | 3.94 | 0.03 | -58.59 |
| NULL | 3 | 128.27 | 4.18 | 0.03 | -60.34 |
| TEMP | 4 | 128.60 | 4.51 | 0.02 | -58.87 |

Trophic level 2 absolute biomass top candidate model

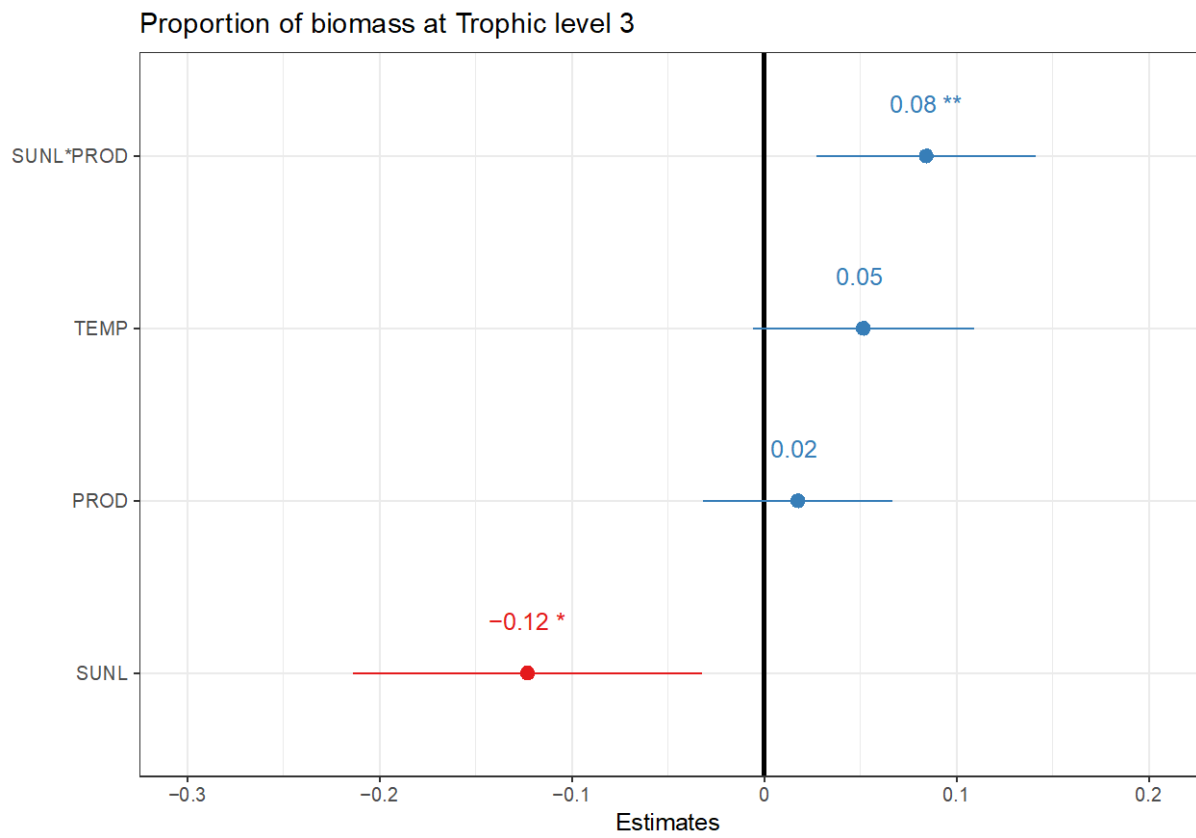
The highest ranked linear model (F statistic (df(1,15): 279.90, $p < 0.001$) had an adjusted R^2 of 0.23 and so had little predictive power to explain the variation in this biomass metric. As model performance was low, the effect sizes are not plotted.

Trophic level 3 – proportional biomass model performance

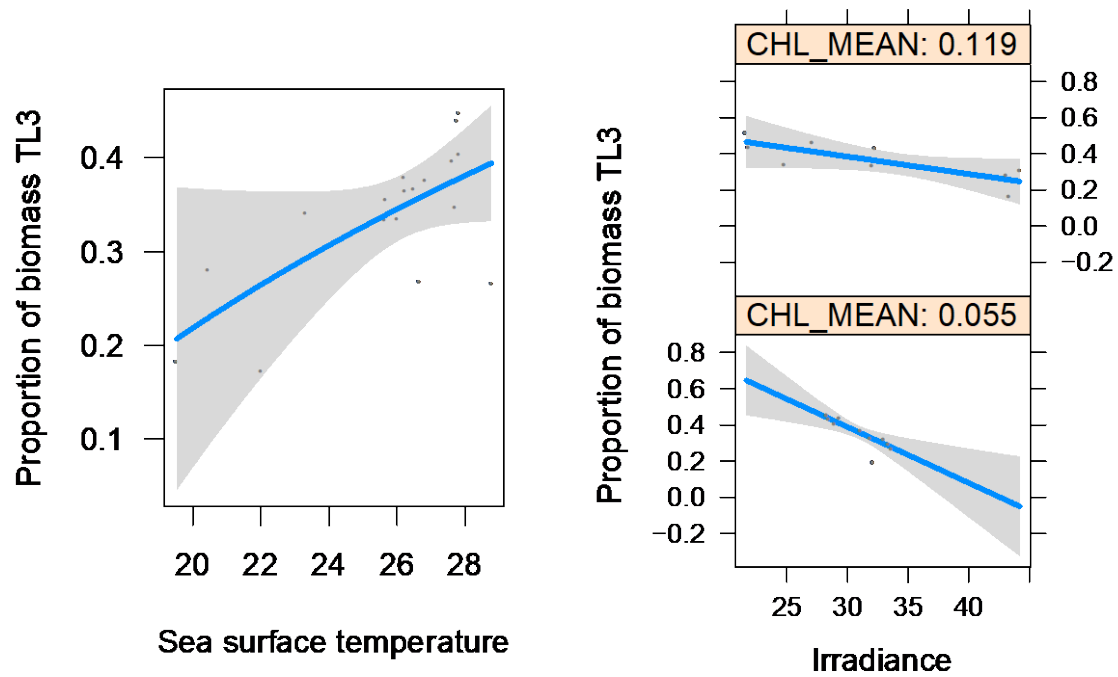
| Model | K | AICc | d | w | LogL |
|---------------------------|----------|---------------|-------------|-------------|--------------|
| SUNL * PROD + TEMP | 6 | -44.13 | 0.00 | 0.31 | 31.30 |
| PROD | 3 | -43.72 | 0.41 | 0.25 | 25.61 |
| NULL | 2 | -42.63 | 1.51 | 0.15 | 23.67 |
| PROD + TEMP | 4 | -41.12 | 3.01 | 0.07 | 25.89 |
| SUNL | 3 | -41.06 | 3.07 | 0.07 | 24.28 |
| SUNL + PROD | 4 | -40.61 | 3.52 | 0.05 | 25.64 |
| TEMP | 3 | -40.10 | 4.03 | 0.04 | 23.80 |
| SUNL + TEMP * PROD | 6 | -39.28 | 4.85 | 0.03 | 28.87 |
| SUNL + PROD + TEMP | 5 | -38.16 | 5.98 | 0.02 | 26.22 |
| SUNL + TEMP | 4 | -38.04 | 6.10 | 0.01 | 24.35 |
| SUNL * TEMP * PROD | 9 | -36.91 | 7.23 | 0.01 | 36.45 |
| SUNL * TEMP + PROD | 6 | -33.98 | 10.15 | 0.00 | 26.22 |

Trophic level 3 proportional biomass top candidate model effect size plots

Effect size plot from highest ranked linear model (F statistic (df 4,15): 4.29, $p = 0.02$) with an adjusted R^2 of 0.41. Dots represent mean effect sizes, lines are the 95% confidence limit. Limits that span the vertical line indicate no effect.



Trophic level 3 – proportional biomass – highest ranked model plots. Irradiance
(Einsteins $\text{m}^{-2} \text{d}^{-1}$), CHL_MEAN = chlorophyll a (mg m^{-3}), sea surface temperature ($^{\circ} \text{Celsius}$)



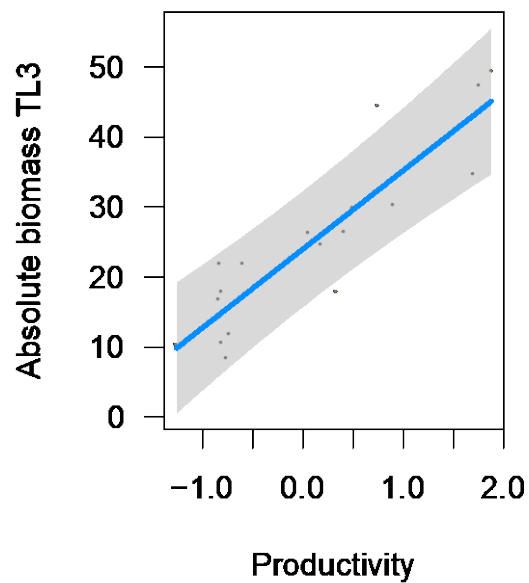
Trophic level 3 – absolute biomass model performance

For the biomass of trophic level three, the Akaike's Information Criterion ranking of models with and without a random effect identified the mixed effects model as the best fit. The candidate models were then fitted with Province as a random effect.

| Model | K | AICc | d | w | LogL |
|--------------------|------------|--------------|------------|------------|--------------|
| PROD | 4.0 | 138.4 | 0.0 | 0.6 | -63.8 |
| PROD + TEMP | 5.0 | 140.3 | 1.9 | 0.2 | -62.9 |
| SUNL + PROD | 5.0 | 141.5 | 3.1 | 0.1 | -63.5 |
| SUNL + PROD + TEMP | 6.0 | 144.7 | 6.2 | 0.0 | -62.8 |
| SUNL * PROD + TEMP | 7.0 | 146.3 | 7.9 | 0.0 | -61.1 |
| SUNL + TEMP * PROD | 7.0 | 149.1 | 10.7 | 0.0 | -62.5 |
| SUNL * TEMP + PROD | 7.0 | 149.8 | 11.4 | 0.0 | -62.8 |
| SUNL | 4.0 | 149.9 | 11.5 | 0.0 | -69.5 |
| SUNL + TEMP | 5.0 | 152.8 | 14.4 | 0.0 | -69.1 |
| NULL | 3.0 | 156.1 | 17.7 | 0.0 | -74.3 |
| TEMP | 4.0 | 159.1 | 20.7 | 0.0 | -74.1 |
| SUNL * TEMP * PROD | 10.0 | 166.2 | 27.8 | 0.0 | -59.3 |

Trophic level 3 – absolute biomass – highest ranked model plots.

The highest ranked linear mixed model that had a conditional R^2 of 0.84 (variance explained by entire model) and marginal R^2 of 0.60 (variance explained by fixed effects). The productivity coefficient estimate was 11.22 (standard error: 1.83, t-value=6.11 $p < 0.01$), with the Province random effect intercepts of Hawaii (14.83), Central Polynesia (26.68) and the Tropical NW Pacific (30.40). Productivity = chlorophyll a (mg m^{-3}).



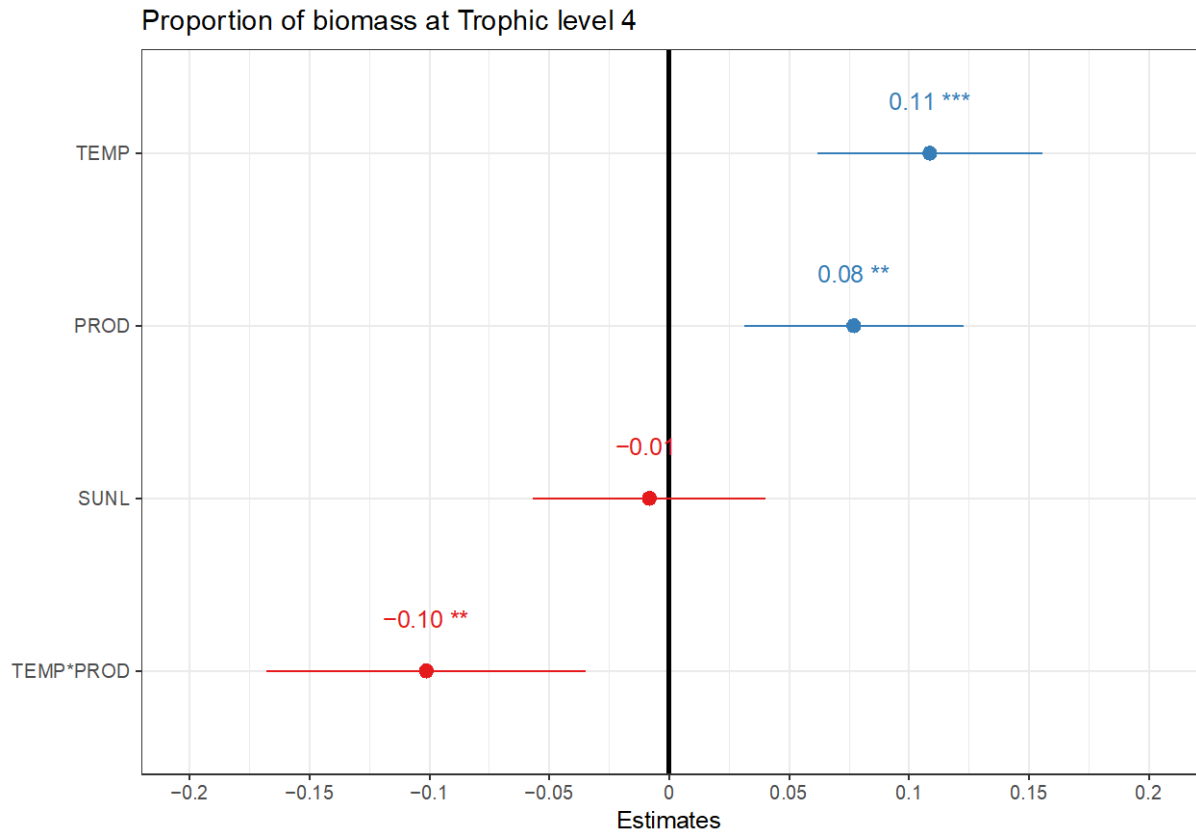
Trophic level 4 – proportional biomass model performance

Table of summary statistics for models fitted showing number of estimated parameters (k), variance explained (adjusted R²), delta AICc and AICc weights – corrected for small sample size. Model name contains variables fitted: '+' for additive effects, '*' for interactions.

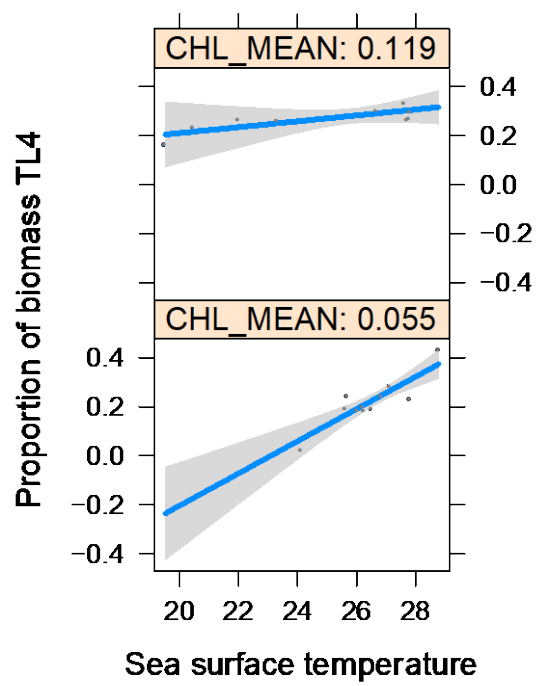
| Model | K | AICc | d | w | LogL |
|---------------------------|-------------|---------------|-------------|-------------|--------------|
| SUNL + TEMP * PROD | 6.00 | -55.36 | 0.00 | 0.65 | 36.91 |
| TEMP | 3.00 | -52.41 | 2.94 | 0.15 | 29.96 |
| PROD + TEMP | 4.00 | -51.95 | 3.40 | 0.12 | 31.31 |
| SUNL + TEMP | 4.00 | -49.86 | 5.50 | 0.04 | 30.26 |
| SUNL + PROD + TEMP | 5.00 | -48.91 | 6.45 | 0.03 | 31.60 |
| SUNL * TEMP + PROD | 6.00 | -46.49 | 8.87 | 0.01 | 32.47 |
| SUNL | 3.00 | -45.78 | 9.57 | 0.01 | 26.64 |
| SUNL * PROD + TEMP | 6.00 | -44.76 | 10.59 | 0.00 | 31.61 |
| SUNL + PROD | 4.00 | -43.18 | 12.18 | 0.00 | 26.92 |
| SUNL * TEMP * PROD | 9.00 | -39.69 | 15.66 | 0.00 | 37.85 |
| NULL | 2.00 | -39.39 | 15.97 | 0.00 | 22.05 |
| PROD | 3.00 | -37.21 | 18.14 | 0.00 | 22.36 |

Trophic level 4 proportional biomass top candidate model

Effect size plot from highest ranked linear model (F statistic (df 4,15): 12.82, $p = <0.01$) with an adjusted R^2 of 0.73 Dots represent mean effect sizes, lines are the 95% confidence limit. Limits that span the vertical line indicate no effect.



Trophic level 4 – proportional biomass – highest ranked model plots. Irradiance ($\text{Einsteins m}^{-2} \text{d}^{-1}$), CHL_MEAN = chlorophyll a (mg m^{-3}), sea surface temperature ($^{\circ}\text{C}$).



Trophic level 4 – absolute biomass model performance

For the biomass of trophic level four, the Akaike's Information Criterion ranking of models with and without a random effect identified the mixed effects model as the best fit. The candidate models were then fitted with Province as a random effect.

Table of summary statistics for models fitted showing number of estimated parameters (k), variance explained (adjusted R²), delta AICc and AICc weights – corrected for small sample size. Model name contains variables fitted: '+' for additive effects, '*' for interactions.

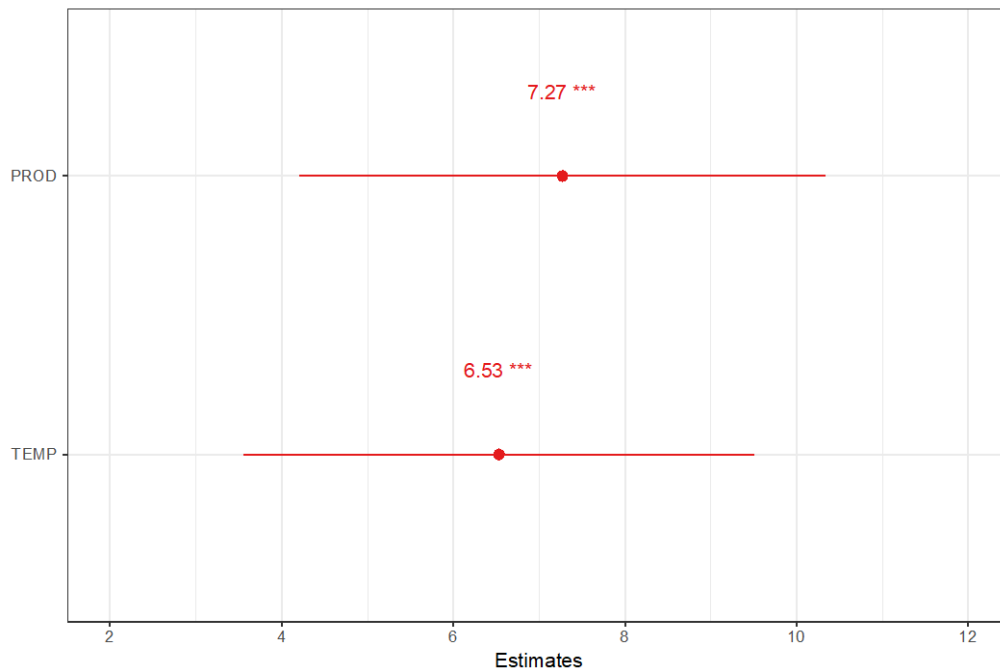
| Model | K | AICc | d | w | LogL |
|--------------------|-------|--------|-------|------|------|
| PROD + TEMP | 5.00 | 136.72 | 0.00 | 0.62 | 0.62 |
| PROD | 4.00 | 140.33 | 3.61 | 0.72 | 0.72 |
| SUNL | 4.00 | 140.48 | 3.76 | 0.82 | 0.82 |
| SUNL + PROD + TEMP | 6.00 | 141.11 | 4.38 | 0.89 | 0.89 |
| SUNL + PROD | 5.00 | 141.34 | 4.62 | 0.95 | 0.95 |
| SUNL + TEMP * PROD | 7.00 | 143.68 | 6.96 | 0.97 | 0.97 |
| SUNL + TEMP | 5.00 | 144.22 | 7.50 | 0.98 | 0.98 |
| NULL | 3.00 | 145.77 | 9.05 | 0.99 | 0.99 |
| SUNL * PROD + TEMP | 7.00 | 146.06 | 9.34 | 0.99 | 0.99 |
| SUNL * TEMP + PROD | 7.00 | 146.22 | 9.50 | 1.00 | 1.00 |
| TEMP | 4.00 | 148.39 | 11.67 | 1.00 | 1.00 |
| SUNL * TEMP * PROD | 10.00 | 156.90 | 20.17 | 1.00 | 1.00 |

Trophic level 4 proportional biomass top candidate model

The highest ranked linear mixed model had a conditional R² of 0.71 (variance explained by entire model), with the marginal R² being the same 0.71 (variance explained by fixed effects). Dots represent mean effect sizes, lines are the 95% confidence limit. Limits that

span the vertical line indicate no effect.

Absolute biomass at Trophic level 4



Trophic level 4 – absolute biomass – highest ranked model plots. Irradiance (Einsteins $\text{m}^{-2} \text{d}^{-1}$), CHL_MEAN = chlorophyll a (mg m^{-3}), sea surface temperature ($^{\circ} \text{Celsius}$).

